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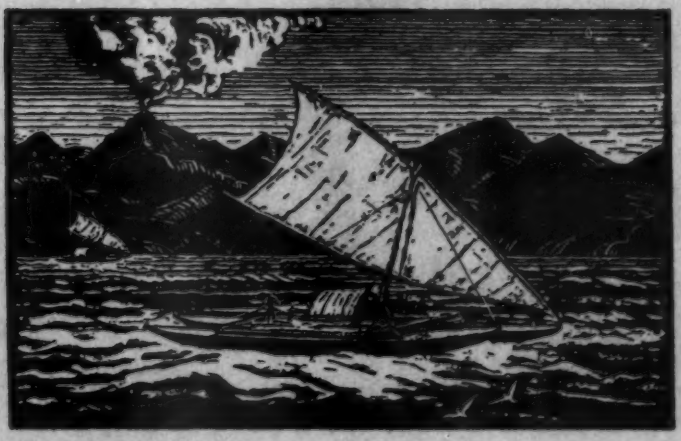
PACIFIC SCIENCE

A QUARTERLY DEVOTED TO THE BIOLOGICAL AND PHYSICAL SCIENCES OF THE PACIFIC REGION



IN THIS ISSUE: Collins—*The Cayenne Pineapple* • Schwabe—*Life History of* Oxyspirura mansoni • Akamine—*Viability of Forest Tree Seeds* • Marples—*Pacific Symphytognathid Spiders* • Webster—*Polynesian Species of* Myoporum • Hubbs—Carcharhinus longimanus *in the East-Central Pacific* • Neal—*Flowers of* Cassia fistula • Schwartz and Schwartz—*The Lace-necked Dove in Hawaii* • NOTES

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HONOLULU, HAWAII

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PACIFIC SCIENCE, a quarterly publication of the University of Hawaii, appears in January, April, July, and October. Subscription price is three dollars a year; single copies are one dollar. Check or money order payable to University of Hawaii should be sent to PACIFIC SCIENCE, Office of Publications, University of Hawaii, Honolulu 14, Hawaii. Reprints of articles from Volumes I and II are available to subscribers.

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Notes on the Origin, History, and Genetic Nature of the Cayenne Pineapple[1]

J. L. COLLINS[2]

ALTHOUGH PLANTS AND FRUITS of the pineapple had been carried from America to Europe a number of times following their discovery by Columbus in 1493, it was almost 100 years before they were successfully grown in Europe. They were first grown to fruiting in Holland about 1690 and in England some 30 years later, following the development of artificial heating of glasshouses.

Thereafter, a great rivalry and enthusiasm developed in the growing of pineapples by the gardeners of the large estates in England and on the continent. They imported varieties from America, exchanged varieties among themselves, and in some instances developed new varieties by growing the seeds which were occasionally found in their fruits or were obtained from the West Indies. As a consequence of this general interest in the growing of pineapples, the horticultural journals of the times frequently carried articles or notices concerning the culture of this fruit.

Like a number of important agricultural crops, the Cayenne variety of the pineapple, *Ananas comosus* (L.) Merr., appeared upon the horticultural scene with no definite record of the manner or the place of its origin. The first reference in the literature to the Cayenne variety appears to be the short notice carried in the *Gardeners' Chronicle* (England) of March 6, 1841, under the column heading of "Foreign Correspondence," as follows:

Paris, Feb. 4, 1841. As information is continually demanded by horticulturists regarding pines, perhaps a few words as to the varieties in request in Paris and the mode of culture may not be unacceptable. The Potager, or Royal Kitchen Garden Versailles has the merit of producing this and other fruits in the greatest perfection. . . . The pinery consists of a vast number of pits, succession and fruiting houses, the whole of which are heated with hot water; it contains about 2000 plants among which are fine specimens of Queens, Cayenne Lisse and Espineux, Black Jamaica . . . in all about 40 varieties. Only four kinds are considered desirable for general cultivation; of these, however, more than 1000 plants are annually fruited, namely 700 Queens and 300 Cayennes, Endville, and Providence. The Cayenne, both smooth and prickly, is of an excellent flavor and weight on the average from 9 to 12 pounds.

This article continues to record the names of the three principal growers, or nurserymen, for the French market, one each in Paris, Versailles, and Meridon, who list Cayenne plants along with some other varieties.

From this date, 1841, we trace the history of the Cayenne variety and map its distribution in geography and time.

In this first reference to the Cayenne variety, mention is made of the smooth-leaved and spiny-leaved forms. Genetic studies in Hawaii (Collins, 1936: 467) have shown that the smooth-leaved type infrequently produces spiny leaves; if we can judge from this modern behavior, then we can assume that the original Cayenne variety had smooth-edged leaves and also produced mutations giving rise to the spiny-leaved form as bud sports.

[1]Published with the approval of the Director as Miscellaneous Paper No. 48 of the Pineapple Research Institute of Hawaii, Honolulu, Hawaii. Manuscript received August 23, 1950.

[2]Department of Genetics, Pineapple Research Institute of Hawaii.

In the *Gardeners' Chronicle* for January 6, 1844, we find another reference to Cayenne in the section on "Notices to Correspondents," as follows: "The Cayenne pine is from French Guiana; cannot state its price, that is the affair of the nurseryman. . . ." A reader of this journal had obviously written to the editor inquiring about the place of origin of Cayenne and the price of plants, and the editor's reply indicates that it had been imported from French Guiana.

In a description of the Cayenne variety in "The Pineapple Manual" (Anonymous, *ca.* 1870), we find the statement that "This fine variety was imported from Cayenne many years ago and is now cultivated in many places."

These scattered and brief references, together with whatever weight may be given because of the name it bears, point rather clearly to Cayenne in French Guiana as the place from which this variety was introduced into France some time before 1840.

The fact that three French nurserymen in 1841 had sufficient material to offer Cayenne plants in their catalogues indicates its presence in France for a number of years previous to that date. In the "Pineapple Manual" mentioned above, the statement is made that "Cayenne is not very free in producing suckers." At the present time we consider that healthy plants will produce an average of about four reproductive shoots each in a 2-year growth period. The rate of increase from a small beginning would be very slow and could well require 15 or more years to produce enough plants so that three nurserymen could offer them for sale. Accordingly we may assume that a few plants may have reached France around 1820 to 1825.

MIGRATIONS OF THE CAYENNE VARIETY

With the distribution of plants to nurserymen in France, Cayenne soon became a favored variety in Europe because of its large, well-shaped fruits, good color, and fine flavor, although the Queen variety was also widely grown and well received. The earlier distribution of Cayenne to other countries appears to have stemmed from England and not directly from France. This early distribution from England is also emphasized by its early appearance in some of the British colonies, it having reached Australia by 1858 and Jamaica in 1870, although it came to Jamaica via Florida. In Australia its development was fairly rapid and from 1890 to 1895 that country was able to furnish many slips and suckers for expanding the pineapple industry in the Hawaiian Islands, although the first Cayennes came to Hawaii from Florida in 1885 and Jamaica in 1886.

The decade from 1885 to 1895 was a period of accumulation of the Cayenne variety in the Hawaiian Islands. Introductions of pineapple plants were made from 11 different tropical countries (Florida, England, Jamaica, Bahamas, Trinidad, Puerto Rico, Mexico, Australia, Singapore, Samoa, and Algeria) four of which were known to have included the Cayenne variety. It is possible that it may have been included in shipments from other countries as well, but the records do not list the varieties in some importations (Collins, 1934: 129).

Figure 1 shows two major centers of distribution of the Cayenne variety to other areas. England played this role during the last half of the nineteenth century, although the first European propagation was accomplished in France. Hawaii has been a major source of distribution during the first half of the twentieth century. It was doubtless sent to still other countries from these three major centers of distribution, but at present we do not have complete records. For instance, it was imported from Ceylon into South Africa, but we do not know how it reached Ceylon.

THE ORIGIN OF CAYENNE

The discussion of the Cayenne variety up to this point is based upon documentary evidence. In trying to trace the origin of the Cayenne pineapple beyond the realm of

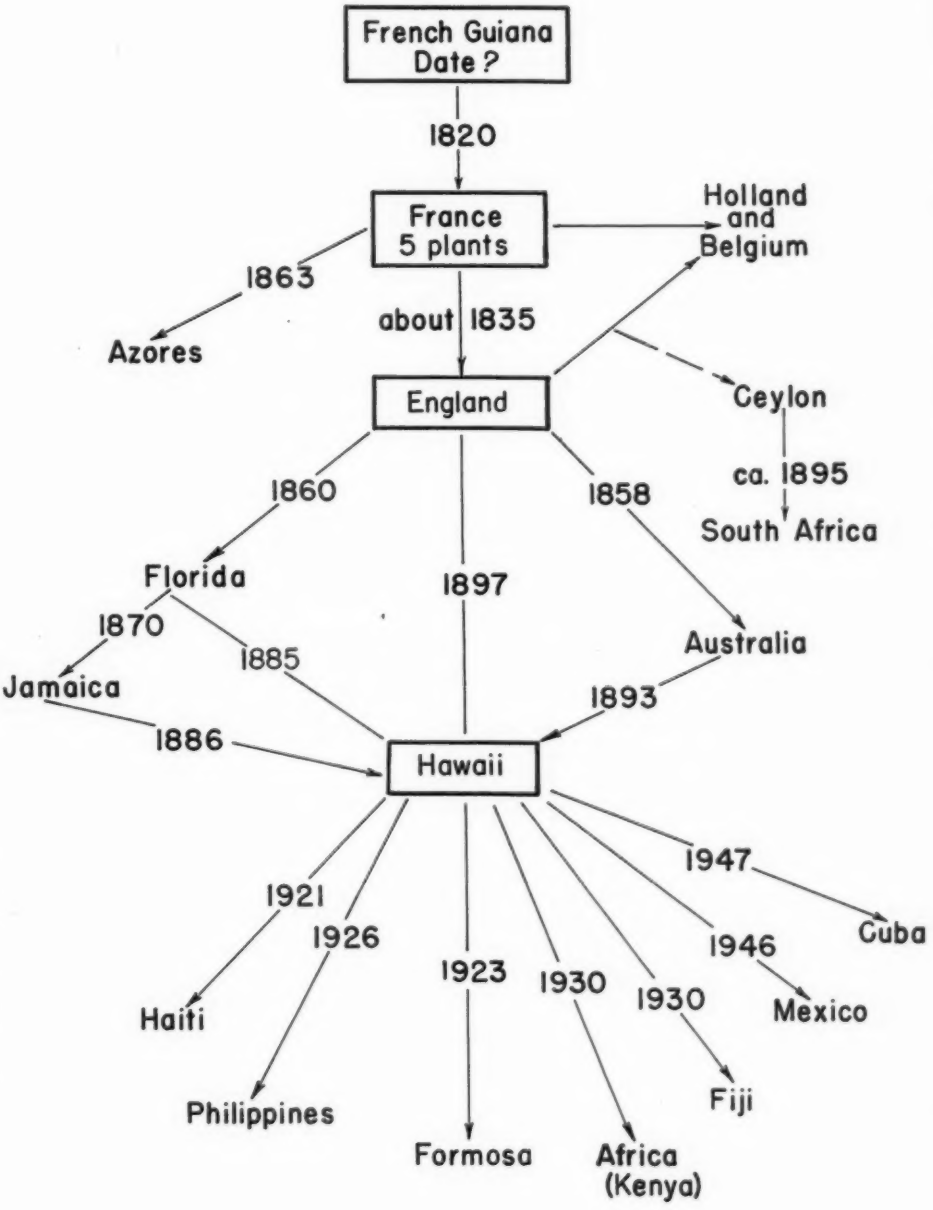

FIG. 1. Distribution of Cayenne following its introduction into France in 1820. Two major centers for distribution appear: first England and then Hawaii.

definitely known or documented history, certain additional conclusions regarding its still earlier history have been based upon circumstantial evidence.

As has already been stated, some of the early horticultural journals in England mentioned that the Cayenne variety had been imported from French Guiana. The name it bears is also circumstantial evidence for that conclusion. This latter statement is based upon the frequency with which plants, particularly the pineapple, are given names according to the place from which the varieties are obtained, even though they already possess local names. Among pineapples there are a number of varieties named after geographical areas in the West Indies and South America. Among these may be mentioned the following:

WEST INDIES	SOUTH AMERICA
Antigua	Bahia
Providence	Esmeralda
Jamaica	Pernambuco
St. Kitts	Taboga
Cuban	Surinam
Havannah	Trinidad
Puerto Rico	Demerara

In the hope that further knowledge regarding the history of the Cayenne variety might be found in French Guiana, a search was made of the botanical literature for reports of plants and plant collections in the northern part of South America. This search disclosed the information that in 1819 the French government sent an expedition to the French colonial possessions in America and the Pacific Ocean area to collect plants and seeds for the French botanical gardens at Paris and Versailles. Samuel Perrottet, the botanist on this expedition, filed a report of the plants collected, in which he records finding a new variety of pineapple growing at Cayenne, in French Guiana, having spineless leaves (the others in the region having spiny leaves) and delicately flavored fruits averaging about 20 pounds in weight (Perrottet, 1825: 103).

He collected and sent to Versailles five plants of this variety in 1820. This date fits in well with that which we have suggested above as being about the time the Cayenne variety is presumed to have been introduced into France.

The description, as it appeared in Perrottet's report, is included here as a part of the history of this variety, with a free translation following it.

Bromelia mai-pouri. Perr. Cette nouvelle espèce d'*ananas* provident de Cayenne; cinq plantes ont été, comme je l'ai dit déposés au jardin des primeurs à Versailles. Le mai-pouri n'a point les feuilles armées de dents comme ses congénères; ses fruits, d'un manger fort délicat, pèsent d'ordinaire 10 kilogrammes (20 livres), et sont très-beaux. M.

This new species of *Ananas* was procured from Cayenne; there were five plants as I have said, deposited in the garden of new varieties at Versailles. The mai-pouri does not have spiny leaves like its relatives; its fruits, of a very delicate flavor, weigh on an average 10 kilograms (20 pounds) and are very fine.

The description given by Perrottet is in itself not sufficient to establish the identity of "*Bromelia mai-pouri*" and the Cayenne variety. In fact, the 20-pound *average* weight of fruit mentioned by Perrottet is difficult to believe of any variety of pineapple and must represent an error in the record. The varieties Trinidad and Cabezona were reported to have fruits sometimes reaching 20 to 24 pounds, but there is no other reference to a variety having an average fruit weight anywhere near 20 pounds.

In commenting upon this description of *Bromelia mai-pouri*, Dr. L. B. Smith, of the National Museum in Washington, D. C., remarked that it looked as if someone made a major error between collection and publication. An inquiry concerning these plants sent to the Natural History Museum in Paris resulted in information that no herbarium specimens now existed of this Mai Pouri variety, but that they were considered the same as Smooth Cayenne in 1850 by Gautier, "the famous grower of Parisian pineapples." The

director of the museum stated that the duplication of names had been published, although the term "Mai Pouri" remains an unsupported name.

The supporting evidence of the date of its introduction into France and the postulated date based on the offering of plants for sale by nurserymen in 1841, together with the statement that Gautier believed the two to be identical in 1850, leads us to conclude that the five plants collected by Perrottet in 1820 represent the beginning of the Cayenne variety in France.

How did this variety get started in French Guiana? This question cannot now and perhaps may never be answered with certainty. The collection of five slips sent to France in 1820 we believe to be of the variety now known as Cayenne. Some time after it reached France it was given the name it now bears.

The name used by the French botanist in his report is somewhat confusing, since he calls it a new species of *Ananas*, yet listed it as *Bromelia*, a closely related genus in the pineapple family. However, Perrottet probably used the name given to him at the time he collected it. The name "Mai Pouri," by which this variety may have been known in French Guiana, probably followed the pattern of indicating the place from which it originated when it first appeared in French Guiana. The quest of the origin of the Cayenne was then continued in a search for a geographical area or locality having the name "Mai Pouri."

In Colombia, at the junction of the Triparro River with the Orinoco River, is a small village called "Maipures." In this region, and in the watershed of the Venturari River in Venezuela, also a tributary of the Orinoco, lived the Maipure tribe of Indians. We now believe that the Cayenne pineapple originated in the interior region of Venezuela long occupied by the Maipure tribe of Indians, and that it was probably grown and used by them for a long period of time (Fig. 2). Velez (1946: 427), who recently traveled through the upper Orinoco River basin, states that the Piaroa Indians have had under cultivation since time immemorial several pineapple varieties which yield large, well-flavored fruits.

Another circumstance which may also have a connection with Maipure pineapple concerns the Esmeralda pineapple variety, grown in Mexico. This variety is very similar, if not identical, to the Cayenne variety. Esmeraldas is the name of a small village at the mouth of the Esmeraldas River in northern Ecuador, in South America. The Maipure pineapple could have been carried from Venezuela or Colombia into the Esmeraldas region of Ecuador and thence into Mexico, where it was given the name of the place from which it had most recently come. We have no indication that it was known as Maipure while being grown in Ecuador, but there is good evidence that the Esmeralda and the Cayenne are the same variety.

How long had this variety been grown in the country of the Maipure Indians and why was it not found by Europeans at an earlier date? To the first question there is no definite answer. We suspect that the history of this variety may extend back into the antiquity of American civilizations along with such notable plants as corn, tobacco, and potatoes.

To the second question a logical answer is apparent. That area of South America is even today largely unexplored, partly because it has long been inhabited by Indians who have had little contact with outside people and because of the difficulty of travel in this little-frequented and still primitive area. The Maipure Indians, who at one time roamed over this area, no longer exist as a distinct ethnic group.

Sir Walter Raleigh, who conducted an expedition in 1595 up the Orinoco River for about 200 miles, reported having received quantities of pineapples from the Indians in the deep interior of the country. The village of Maipure on the Orinoco River is at the place now marked on maps as the head of navigation. This is some 200 miles farther up the Orinoco than the place reached by Ra-

leigh. Could Sir Walter Raleigh and his men have been the first white men to find and eat the Cayenne pineapple?

If the Cayenne pineapple originated in the Maipure Indian country, the parent variety or species may still be present as a part of the native vegetation. Other members of the hybrid population of which our Cayenne variety was a member may still be among those used by the Indians. Could some of the sibs of the Cayenne variety be better fitted for large-scale commercial production? Could some of the sibs have inherited resistance to diseases which Cayenne failed to obtain? Could some of the sisters of Cayenne have inherited two or more genes for yellow flesh color, where Cayenne obtained only one?

These are some of the questions which have been raised by this study of the origin of the Cayenne variety of pineapple, to which answers should sometime be obtained.

VARIATIONS WITHIN THE CAYENNE VARIETY

Two types of hereditary variations, which may be designated as strain differences and mutations, exist within the variety.

Strain differences

The term "strain" is used here to indicate hereditary differences in fruits or plants within a variety when the manner of origin of these differences is not known. A long time ago growers of this variety recognized strain differences. The *Journal of the Jamaica Agricultural Society* (about 1900) carried a statement that there was a good and a poor kind of Smooth Cayenne and that the latter was also known as the Honolulu kind!

Captain John Kidwell, an early pioneer of the pineapple industry in Hawaii, stated (Kidwell, 1904) that there were two distinct types in Hawaii, and that he considered one much superior to the other. The poor type of Cayenne, according to his statement, had been imported from Queensland, Australia, under the name of Smooth Cayenne. He described it as having a very large plant producing fruits weighing from 7 to 15 pounds and numerous slips on the peduncle beneath the fruit. The fruits, while of good quality, were conical in shape and possessed a very large core. The other type, which he called the "true" Cayenne, was similar in appearance, but the plants were smaller and produced fruits from 5 to 7 pounds in weight. This type did not produce slips on the peduncle beneath the fruit. As a consequence of this latter characteristic, this good strain was necessarily propagated from suckers and the crowns.

In 1887 a report of the United States Department of Agriculture on tropical and subtropical fruits mentions three kinds of Cayenne being grown in the Key West region of Florida. These were listed as Smooth Cayenne, Spine-leaved Cayenne, and Thompson's Smooth Cayenne. No description of the third kind was given, but its listing as a separate strain indicates that it may have been different in some respect from the others.

In Hawaii we recognize three strains of Cayenne, all of which produce good canning fruits but differ in some plant and fruit characters. The one used most extensively throughout the Islands is known simply as Cayenne. The second strain, grown mostly on Kauai, is known as the "Hilo" variety, or as the Hilo Cayenne. The Hilo variety differs from Cayenne in at least three characters. The most prominent difference is in the absence of slips in the Hilo variety. It also produces a smaller plant and fruit, with the fruit more cylindrical and of better average quality. It produces more suckers than Cayenne and the plants have a darker green leaf color. These differences are about the same as those Captain Kidwell used to distinguish between Cayenne and what he called the Queensland type. The strain we now call Hilo appears to

FIG. 2. Location of the probable area of origin of the Cayenne pineapple, showing the location of the town of Maipures on the Orinoco River. The Venturari River (Ven. R.) area, for a long time the country of the Maipure Indians, is also shown.

GOODE'S SERIES OF BASE MAPS
HENRY A. LEPPARD, EDITOR

Prepared by Henry M. Leppard
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TABLE 1
CLASSIFICATION OF SOMATIC MUTATIONS IN CAYENNE

FRUIT MUTATIONS

I. Foliar proliferation of the fruitlet
   1. Crowning Beauty
   2. Hour Glass
   3. Slipping Beauty

II. Multiplication of floral organs
   4. Flowering Beauty (increase in petal number)
   5. Multiple sepals and bracts

III. Disappearance of floral structures
   6. Dry fruit (only the floral bract subtending the fruitlet remains)
   7. Bottle Neck (the upper one half to one third of the fruit is like the dry fruit)

IV. Changes in fruit characters
   8. Elongated bracts and sepals
   9. Big eyes
   10. Slender
   11. Elongated fruit
   12. Self seedy
   13. Rough (pointed eyes)
   14. Non-porous flesh
   15. White flowers
   16. Nubbin (dwarf and abnormal fruit—eyes small and distorted, surface very rough) M226

PLANT MUTATIONS

V. Single character changes
   17. Spiny leaves
   18. Absence of anthocyanin
   19. Linear anthocyanin
   20. Blush anthocyanin
   21. Intensified anthocyanin
   22. Albino (no chlorophyll)
   23. Streaked anthocyanin
   24. Waxy (absence of trichomes)
   25. Semi-waxy (reduction in trichomes)
   26. Mealy (increased trichomes)
   27. Few slips (573, M4W)
   28. Increased number of slips (L69)
   29. Multiple crowns
   30. Increased wilt tolerance (resistance)
   31. Increased chlorophyll (LH8)

VI. Multiple character changes
   32. Paper Leaf (degenerate plant)
   33. B.B. (gigas form)
   34. Lanai (short leaf type)
   35. Driver's Dwarf (dwarf)

be identical with the one Kidwell called the "true" Cayenne.

Our third strain is known as the Collar-of-Slips, because of the excessive number of slips produced around the base of the fruit. It has a smaller fruit than the Hilo, is later in maturing its plant and ratoon crops, and is generally considered an undesirable type.

These Cayenne strains have been present as components of the variety for a long, long time. How they originated or which represents the true or original Cayenne cannot now be determined with certainty.

FIG. 3. A plant of the Cayenne variety, showing slips, suckers, and a mature fruit.

Figure 3 shows a typical Cayenne plant with slips, suckers, and a mature fruit.

Mutations

The term "mutation" is applied to new hereditary variations which appear *de novo* in a population of plants or animals, caused by a change in the structure of a chromosome and thus in the hereditary constitution of the individual.

Mutations have occurred in the Cayenne variety, giving rise to a series of new or changed forms; some are so profoundly changed that they no longer show the variety characters, others show only minute changes.

These mutant forms are treated separately from the strains already discussed, principally because we know something about the origin of these mutations and we do not know how the strains originated. It is quite possible that the latter also started as somatic mutations.

The mutations in Cayenne can be conveniently divided into six classes on the basis

of the characters which are altered. Four classes affect the fruit and two classes affect both fruit and plant characters (Table 1).

The mutations listed in the first five classes of Table 1 are relatively slight or small character alterations. They influence one or a few characters and do not, for the most part, represent profound genetic changes, even though the character alteration may be conspicuous. The mutant Crowning Beauty (Fig. 4) is an example of this kind of mutation.

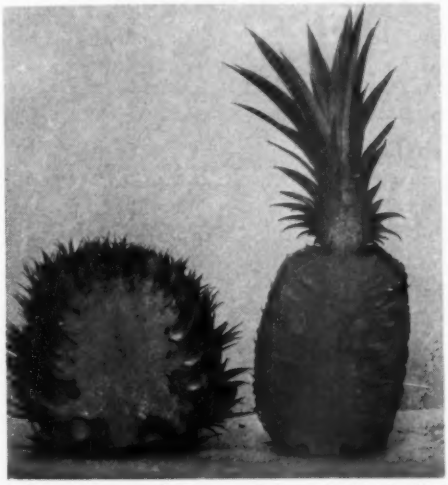

FIG. 4. A normal Cayenne fruit cut in longitudinal section on the right, showing internal structures of core, carpels, and vascular fibers. On the left is the mutant type Crowning Beauty, showing foliar proliferation of the fruitlets and absence of normal carpel structures.

Those in Class VI, however, stand apart from the rest because they represent simultaneous changes in a number of different morphological and physiological characters.

The Lanai type and B.B. mutations (Fig. 5) appear to be complementary to each other in their deviation from the normal variety. They vary from typical Cayenne in opposite directions in at least six characters, shown in Table 2.

TABLE 2
CHARACTERS OF MUTANTS B.B. AND LANAI COMPARED WITH THOSE OF THE NORMAL VARIETY

CHARACTER	VARIATION FROM TYPICAL CAYENNE	
	In B.B.	In Lanai
Leaf number	decreased	increased
Leaf length	increased	decreased
Fruit size	larger	smaller
Fruit maturity	later	same as normal
Plant size	larger	smaller
Spines	more	normal

The Paper Leaf mutant departs so widely from the normal variety in a number of characters that it no longer resembles the Cay-

FIG. 5. A normal Cayenne plant in the center, with the short leaf Lanai mutation on the left and the long leaf one on the right. These represent changes in opposite directions from the normal.

enne at all. It is considered a degenerate type, because of its small, worthless fruit and weakly growing plant. It probably could not survive in field competition with normal plants.

Driver's Dwarf (Fig. 6) has a diminutive form of plant and fruit, combined with collar of slips and an intensified purple anthocyanin pigment in the leaves. This may represent a change from the normal slip type of the Cayenne variety to the collar-of-slip strain. On the other hand, the mutation giving rise to dwarf and increased anthocyanin may have occurred in a collar-of-slip strain plant which was already in the field population. The dwarfing and anthocyanin intensification appear to have been simultaneous changes.

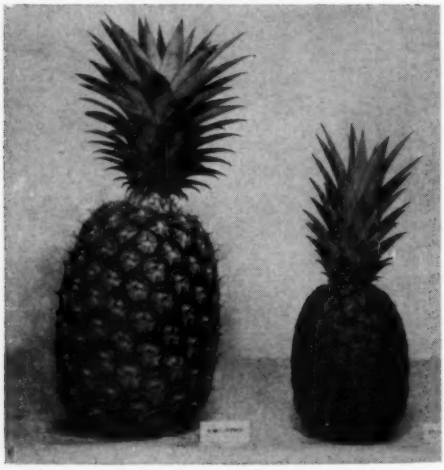

FIG. 6. A normal Cayenne fruit on the left, with a fruit of the mutant Driver's Dwarf on the right.

Discussion of these more obvious mutant types naturally leads to the question of the possible occurrence of other mutations which are less conspicuous and less easily measured. Undoubtedly mutations of this kind take place, but the demonstration of the existence of mutations of slight phenotypic effect is much more difficult, because of overlapping variations of a non-hereditary nature.

Some examples of these small or elusive mutant effects are briefly described to show that at least a few are present in the variety.

Two Cayenne clones were found to show a slightly darker green color, which could be recognized easily when a fairly large group of these were growing adjacent to a group of the normal variety. A clone may be thought of as one plant multiplied many times by vegetative reproduction, and all plants of a clone have identical heredity. Chemical analyses of leaves revealed a higher chlorophyll content in these darker green leaves. A mutation of slight effect on chlorophyll production was probably the origin of these darker green clones.

The elongated fruit mutation listed in Table 1 develops a large number of multiple crowns and fasciated fruits when grown in warm, dry areas, but only normal plants appear in the cool, more moist areas. In this case the additional character of multiple crowns is quite obvious under one environmental condition and disappears (or merges into the normal pattern) when grown under other conditions.

The number of slips produced per plant is a character subject to considerable variation due to differences in the environment during the growth period. This is well illustrated by the effect of relative crowding of plants in the field. Close planting reduces the number of slips, and, conversely, widely spaced plants permit a larger number of slips to develop. Table 3 shows the variation in number of slips resulting from an experimental planting of Cayenne with 10, 12, 14, and 16 inches between plants (that is, with different degrees of crowding).

TABLE 3

EFFECT OF DIFFERENT PLANT SPACINGS ON SLIP PRODUCTION

PLANT SPACING IN INCHES	AVERAGE NUMBER OF SLIPS
10	2.51
12	3.33
14	3.95
16	4.36
Odds — 19 to 1	0.43
Odds — 99 to 1	0.60

Because of the susceptibility of this character to variation due to environmental dif-

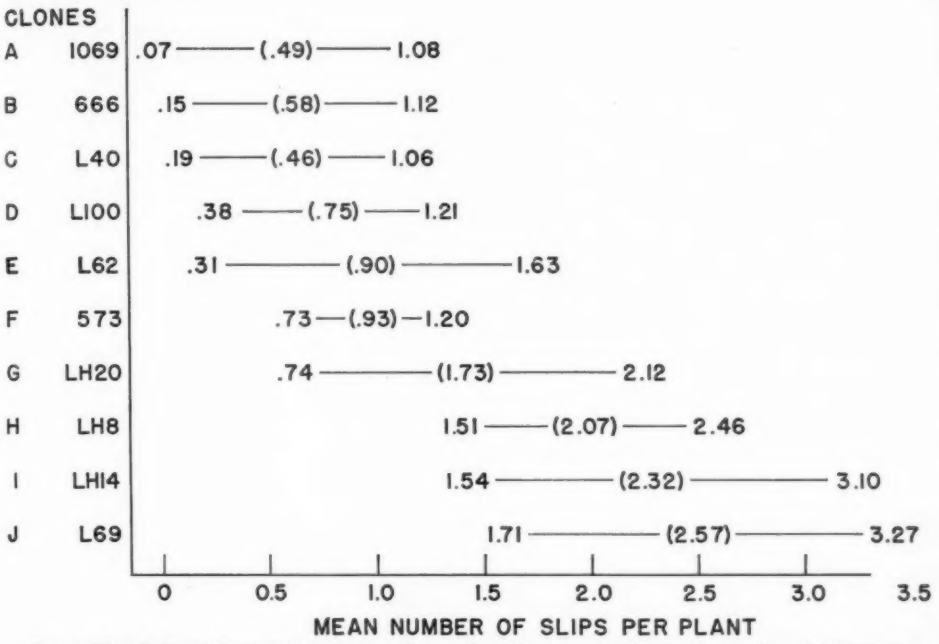

FIG. 7. Ten Cayenne clones showing mean slip numbers for a period of 7 years, together with lowest and highest yearly means.

ferences, the discovery of genetic variations (somatic mutations) which have an effect on slip number is more difficult than locating mutations which are not subject to environmental modification. However, by repeated tests under similar environmental conditions it has been possible to demonstrate the occurrence of mutations affecting number of slips in this variety.

Figure 7 shows the mean number of slips per plant for 10 clones over a period of seven plant crop harvests, together with lowest and highest limits of the yearly means for that period. Five of the clones had a range of annual mean slip number which did not overlap the range of three other clones. Two clones, E and G, had a range of variation which overlapped all the other groups. There can be little doubt about a genetic difference existing between any one of the three high slip-producing clones, H, I, J, and any one of the five low-producing clones, A, B, C, D, and F.

The three high slip-producers, H, I, and J, do not appear[3] to differ among themselves. Clone G, overlapping in its range with both the high and low slip producers, appears to be genetically different from both groups.

These mutant clones can be compared with each other, but should not be compared with the mean of the variety, first because they are a part of the variety and second because—the variety being a mixture of genetic types—random samples would not always include the same distribution of variant types. Furthermore, most Cayenne populations include some plants of the collar-of-slip strain, which produces a very high number of slips.

The somatic mutations in Cayenne include a range of types varying from those having

[3]These conclusions are based upon another replicated plot test which showed significant differences as listed here, and we presume that the causes of the differences were genetic.

marked, easily recognized characters to those differing so slightly that only statistical analyses of quantitative data will identify them.

They are not frequent in occurrence, with the exception of a few which have been shown to be frequently mutating types (Collins, 1936). The mutations discussed here have been collected over a period of 20 years or more and from among millions of normal plants.

This variety is as stable genetically as are vegetatively propagated, highly heterozygous diploid varieties in general. Were this not true, the variety could not have been maintained through this long period of time.

Cayenne is not the single clone it probably was at the beginning. Now it is a collection of clones, all having the same general characters but usually differing in one or a few characters or degrees of expression of characters. The more obvious mutations and those too poorly adapted to survive in the general population have been and are being reduced to small percentages or eliminated. The remaining population heterozygosity consists of minor character alterations which are carried along by asexual propagation in the general mass of cultivated plants. As examples of these latter clonal types, reference can be made to some of those listed in Table 1, such as the clone with less porous fruits, self-seedy types, low and high slip-producing forms, and increased amount of chlorophyll.

As to their value to the organism (in a cultivated variety, positive value in horticulture) these somatic mutations follow the known pattern of randomly occurring mutations; the great majority are either detrimental or of no advantage to the organism. Only three of those which have been studied appear to have possible advantage in pineapple culture, and only two of these, the wilt-resistant mutant and the high slip-producing type, are of possible importance.

TETRAPLOID CAYENNE

The pineapple normally has 50 chromosomes in its somatic cells. This is considered to be the diploid number for the genus *Ananas*. However, tetraploid Cayenne plants having 100 chromosomes were obtained after treating shoot growing points with colchicine solution (Kerns and Collins, 1947). The immediate results from these treatments were various kinds of chimeras of diploid and tetraploid tissues, together with plants which either died early in growth or reverted to normal diploid tissue throughout.

By careful selection of buds from the tetraploid sectors of chimeras during several successive vegetative generations, constant new types which fall into the following three classes on the basis of the amount and location of tetraploid tissue were obtained.

Class 1 was completely tetraploid.

Class 2 was tetraploid except for a diploid epidermis.

Class 3 was diploid except for a tetraploid epidermis.

Classes 1 and 2 were alike in all visible characters. Class 3 was like the normal diploid in all visible characters.

The tetraploid has been compared in Table 4 with the diploid in a number of important characters. The fruit weight is less in the tetraploid and the fruit has fewer eyes than in the diploid. The average eye weight, however, is higher in the tetraploid, showing that the individual eyes of the tetraploid are larger. The Brix (dissolved solids including sugars) of the tetraploid fruit is lower than in the diploid fruit. The characters of fruit acidity, translucence, and vitamin C content are highly variable, so that no significant differences were obtained. These characters are readily altered by different environmental conditions.

Tetraploid plants are taller than diploids, but they have fewer leaves and produce fewer slips. They do not differ in average leaf length, although the tetraploids have wider leaves. The tetraploids also have a higher percentage of water in the leaves and, as a consequence, a lower percentage of dry matter per unit weight of green leaf tissue.

The fruits are seedless, as are the diploids. The chromosomes perform regularly in germ-cell formation, and functional gametes are produced.

Crosses between the Cayenne tetraploid and varietal hybrid tetraploids produce viable seed readily, but crossing with diploid forms produces very little seed; this is similar to the results obtained when varietal hybrid tetraploids are crossed with diploids.

TABLE 4

COMPARISON OF THE FRUIT AND PLANT CHARACTERS IN THE DIPLOID AND TETRAPLOID CAYENNE

CHARACTERS	DIPLOID	TETRAPLOID
Fruit weight (lbs.)	5.8	4.0*
Eye number	140.4	105.6*
Eye weight (gm.)	16.3	16.8*
Brix	15.4	13.8*
Acidity (per cent)	0.71	0.86
Vitamin C	19.2	20.8
Translucence	2.7	2.3
Plant height (cm.)	28.1	30.5*
Number of active leaves	57.6	44.2*
Leaf length (cm.)	65.0	65.2
Leaf width (cm.)	5.4	6.2*
Percentage water in leaves	81.8	83.5*
Percentage dry matter in leaves	18.2	16.5*
Pollen grain diameter (microns)	47.0	64.0*
Stomata size (microns)	22.0	31.0*

*Significant differences.

In many plants, and particularly in ornamentals, valuable horticultural characters are obtained by doubling of the chromosomes (Emsweller, 1948: 570). However, the tetraploid Cayenne is inferior to the diploid form in several important characters (Table 4).

GENETIC NATURE OF CAYENNE

The Cayenne pineapple normally has seedless fruits, although it does produce normal germ cells. The seedlessness results from a condition known as self-incompatibility. Under these conditions the germ, or sex, cells of the same individual do not unite in fertilization to form embryos. Germ cells from two different varieties, Cayenne and Queen, for instance, are mutually compatible and seeds are produced following cross pollination between the varieties.

Inasmuch as inbreeding is thus denied because of self-incompatibility, the studies of the genetic nature of Cayenne have been conducted largely from the results of varietal crossings and from examination of the somatic mutations which have appeared in field populations.

Cayenne has a diploid number of 50 chromosomes; in the somatic cells they appear slightly elongated or almond-shaped (Collins and Kerns, 1931: 140); in the germ cells, they are almost round. While the process of germ-cell production is usually normal, some abnormalities occur. The most frequent abnormality is the formations of germ cells containing 50 chromosomes, which is double the ordinary number of chromosomes in gametes. These appear in the mature sex cells as giant pollen grains and ovules.

In crosses between Cayenne and other varieties, these giant germ cells give rise to occasional hybrids having 75 or 100 chromosomes instead of the normal number of 50 for this species.

The number of these plants whose cells have 75 and 100 chromosomes is far below the expected number on the basis of the percentage of 50-chromosome germ cells produced. This shows that only a small proportion of the plant gametes function in fertilization and that selective fertilization in favor of the normal 25-chromosome gametes takes place.

Hybrid populations resulting from crossing Cayenne with other varieties provide some information regarding the genotype or hereditary constitution of the Cayenne variety.

The variety is heterozygous for many recessive and dominant genes. Table 5 gives some information on the genotype of Cayenne obtained from crossing with other varieties.

INBREEDING IN CAYENNE

In discussing the somatic mutations which have appeared, mention was made of the self-

TABLE 5

THE GENOTYPE OF CAYENNE WITH RESPECT TO CERTAIN CHARACTERS

CAYENNE CHARACTER	CONTRASTING CHARACTER	CAYENNE GENOTYPE	CAYENNE DOMINANCE RELATION
Spiny tip leaves	spiny leaves	Ss	dominant
Spiny tip leaves	piping leaves	pp	recessive
Anthocyanin in leaves	no anthocyanin	Aa	intermediate
Yellow flesh	white flesh	Yy	intermediate
Purple petals	white petals	WW	dominant
Chlorophyll	no chlorophyll	Cc	dominant
Normal fruit	proliferation	*	recessive
Seedless	seedy	*	recessive
Long leaves	short leaves	*	dominant

*Undetermined.

fertile mutation. In this form, the self-incompatibility characteristic of Cayenne is replaced by self-fertility as a result of a dominant mutation, but in all other respects the variety characters remain unchanged.

Inbreeding can now be carried out in the variety by using these self-fertile mutants. Inbreeding is a potent tool for dragging recessive skeletons out of hereditary closets and displaying them in the light of day for all to see. By the use of this tool we have pried out of Cayenne recessive secrets which it has long carried buried within its genotype.

About one fourth of the inbred progeny are semi-lethal and die in an early seedling stage. Another fourth are so weak that they grow very slowly and reach fruiting maturity long after the parent Cayenne. Most of the inbreds are low in vigor, with only a few approaching that of the Cayenne variety. They exhibit a wide variation in fruit and plant types, including many fruit and crown fasciations. The inbred population supplies evidence that Cayenne is not only heterozygous for many recessive and some dominant characters, but that it exhibits heterosis or hybrid vigor.

A number of variations which had appeared in the variety as somatic mutations also appear in the inbred population in numbers indicating Mendelian segregation in a heterozygous genotype.

The general characteristics of the inbred populations supply some evidence regarding the parentage of Cayenne itself. The origin of this variety as a hybrid between any of the known species of *Ananas* can be ruled out, we believe. The parent or parents producing this variety through sexual reproduction must be considered at present as unknown varieties of *A. comosus*, or of such a variety of *A. comosus* and a species of pineapple not known at the present time.

SUMMARY

The Cayenne variety of pineapple was first mentioned in an English horticultural journal in 1841. Evidence is presented to show that it came from French Guiana in 1820. It is presumed to have been grown by the Maipure Indians in the upper Orinoco River valley long before it reached French Guiana. The manner and time of its origin are obscure.

After its introduction into France and England, it became established in many tropical countries during the 100 years between 1840 and 1940.

The genotype of the variety is highly heterozygous and it exhibits hybrid vigor in its growth. The variety is self-incompatible and must be propagated vegetatively. During its long period of vegetative propagation a number of somatic mutations have appeared, including one giving the mutant type self-compatibility. The present Cayenne is a miscellaneous collection of clones. The diploid chromosome number is 50, with 100-chro-

mosome tetraploids obtained by treatment of diploids with colchicine. The tetraploids are inferior to the diploids.

REFERENCES

ANONYMOUS. *Ca.* 1870. The pineapple manual, being a guide to the successful cultivation of the fruit and construction and management of the pinery by contributors to the Journal of Horticulture. London: *Jour. Hort. and College Gardener.*

COLLINS, J. L. 1934. Introduction of pineapple plants into Hawaii and some brief accounts of pioneer pineapple growing. *Pineapple Quart.* 4: 119–120.

——— 1936. A frequently mutating gene in the pineapple, *Ananas comosus* (L.) Merr. *Amer. Nat.* 70: 467–476.

——— and KENNETH R. KERNS. 1931. Genetic studies of the pineapple. I. A preliminary report upon the chromosome number and meiosis in seven pineapple varieties (*Ananas sativus* Lindl.) and *Bromelia Pinguin* L. *Jour. Hered.* 22: 139–142.

EMSWELLER, S. L. 1948. Breeding of ornamental plants. *Amer. Soc. Hort. Sci., Proc.* 51: 565–574.

KERNS, K. R., and J. L. COLLINS. 1947. Chimeras in the pineapple. *Jour. Hered.* 38: 323–330.

KIDWELL, CAPT. JOHN. 1904. The cultivation of pineapples in Hawaii. *Hawaii. Forester and Agr.* 1 (12).

PERROTTET, SAMUEL. 1825. Catalogue raisonné des plantes introduites don les colonies française de Mascareigne et de Cayenne, et de celles rapportées vivantes des mers d'Asie et de la Guyane au Jardin des Plantes de Paris. *Mem. Soc. Linn.* 3(3): 89–151.

VELEZ, ISHMAEL. 1946. Wild pineapples in Venezuela. *Science* 104: 427–428.

Studies on *Oxyspirura mansoni*, the Tropical Eyeworm of Poultry. II. Life History

CALVIN W. SCHWABE[1]

THIS PAPER, the second in a series, presents the results of a study made in Hawaii of the life history of *Oxyspirura mansoni*, the tropical eyeworm of poultry. This nematode has been shown by previous investigators to possess a digenetic life cycle in which it utilizes as the definitive host many species of domestic and wild birds and, as the secondary host, a single species of burrowing cockroach, *Pycnoscelus surinamensis*.

The parasite is widely distributed in the warmer parts of the world. It has been reported from Brazil (de Magalhaes, 1888; Almeida, 1933), China (Cobbold, 1880), Indo-China (Fielding, 1928*b*), Mauritius (Emmerez and Megnin, 1901), Reunion (Ozoux, 1910), British West Indies (Hutson, 1943), Formosa (Kobayashi, 1927), British and Dutch East Indies (Picard, 1929; Fielding, 1928*b*), Florida and Jamaica (Ransom, 1904), Hawaii (Wilcox and McClelland, 1913), Guam (Fielding, 1928*b*), and Samoa (Alicata, personal communication). Its near relative (or synonym), *Oxyspirura parvovum*, has been reported from Australia by Dodd (1909).

Apparently Manson's eyeworm has approximately the same circumtropical distribution as its intermediate host (reviewed in Schwabe, 1949). Neither parasite nor host is known to exist in Hawaii at altitudes exceeding 3,000 feet.

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The eyeworm is considered important economically in many tropical and subtropical areas. The roach is objectionable not only in that it serves as the vector for the eyeworm, but also because it reportedly damages both roots and bark of certain ornamental and crop plants (reviewed by Schwabe, 1949). Previous to this study the development of the larval and adult stages of this parasite was not well known.

MATERIALS AND METHODS

Surinam roaches in all stages of development were easily collected from soil beneath chicken houses and in chicken yards. Because the incidence of natural infection with the parasite among such roaches approached 100 per cent, only laboratory-raised nymphs were employed in the experimental infections.

Adult *Pycnoscelus surinamensis* females were housed individually in 4-inch glass stacking dishes. A 3-inch disk of filter paper was placed in each dish to provide a hiding place for the roaches during the daytime. Nymphs, isolated at birth, were housed together in the same manner as the adults. The roaches thrived on a diet of whole-wheat bread and water.

Embryonated eggs for infecting laboratory-raised roaches were obtained by macerating gravid female worms. This procedure proved more satisfactory than the involved method of concentration and separation of embryonated eggs from the feces of infected birds.

The gravid worms were taken from the eyes of infected chickens obtained from poultry farms in Manoa Valley and Waialae, Hono-

lulu. The parasites were removed from the eyes of the birds by holding the head rigid and inserting the tips of a pair of dull-pointed forceps beneath the nictitating membrane. Worms thus obtained usually survived for at least 24 hours in physiological saline at room temperature.

Young nymphs to be infected were first isolated without food or water in clean stacking dishes for at least 48 hours. Nymphs which were dead or enfeebled after this treatment were removed. Gravid female eyeworms were macerated in a drop of water to free the eggs from the vagina and uteri. The entire mass was then soaked up with a small bread crumb. The starved nymphs rapidly ate the moistened bread. It was later found that the nymphs would just as readily consume living female worms so this method of infection was adopted.

A roach to be examined was pinned, dorsal side downward, on a paraffin block. The head was severed with a sharp scalpel and the posterior abdominal segment was teased from the remainder of the abdomen with fine dissecting needles. The rectum remained attached to this segment and the entire alimentary tract was withdrawn in this manner. The alimentary tract and the remainder of the roach were each placed in a few drops of physiological saline solution on separate clean glass slides. Free third-stage larvae, if present, could, with the unaided eye, then be seen wandering about on the slide. Encysted second- and third-stage larvae were readily observed entangled in the Malpighian tubules or attached elsewhere along the alimentary canal, particularly in the region of the rectum.

To observe the late first-stage larvae, the abdominal fat was dissected away from the body wall, placed in a drop of physiological saline solution, and examined beneath a cover slip with the aid of a compound microscope.

In examinations for early first-stage larvae, the crop and esophagus were severed from the remainder of the alimentary canal, teased apart, and examined as a wet mount with a compound microscope. This procedure was repeated on separate slides for the midgut and hindgut.

First-stage larvae were examined as live wet mounts or were stained vitally with methylene blue or fixed in Bouin's solution. Second- and third-stage larvae were examined alive by compressing the cyst beneath a cover slip or by freeing the larvae from the cysts and fixing them in Bouin's solution. Fourth-stage larvae were killed in Bouin's solution and examined as wet mounts.

When living larvae were too active for study they were anesthetized by a crystal of chloral hydrate introduced beneath the cover slip.

The chickens used in these experiments were all hybrid stock (Rhode Island Red × New Hampshire Red) obtained at the age of 2 weeks from the Department of Poultry Husbandry, University of Hawaii. They were housed on wire and fed commercial growing mash.

Third-stage larvae were first obtained in the laboratory by the dissection of large numbers of infected roaches. Inasmuch as this consumed so much time and the larvae were not obtained in the numbers desired, a more satisfactory method was devised. It was observed that when infected roaches were torn apart and placed in physiological saline solution, heated to approximately 37° C., the larvae immediately began to migrate from the tissues of the roaches and to settle to the bottom of the container. This behavior of the larvae suggested the use of the Baermann apparatus, with which an ample supply of infective larvae was readily obtained.

THE ADULT EYEWORM

The sexually mature worms are found beneath the nictitating membranes and in the conjunctival sacs and naso-lacrimal ducts of domestic chickens, ducks, and a number of other wild and domesticated birds.

Anatomy of the adult eyeworm

The adult *Oxyspirura mansoni* is a slender,

TABLE 1

REPORTED MEASUREMENTS OF ADULT FEMALE EYEWORMS

MEASUREMENT	SCHWABE (Oahu, T.H.) 1948–49	RANSOM (Florida) 1904	MAGALHAES (Brazil) 1888	SWEET (Australia) 1910*	FIELDING (Australia) 1928*
Length†	15–17	12–18	16.2‡	13.5–20	15.5–17
Width (ant. end)	69.1–75	50			
Width (max.)	369–538	400–430		270–390	270–420
Width (at anus)	92‡	90–100			
Esophagus length†	1.55‡	1.5			
Esophagus width (post. end)	107‡	80–100			
Intestine width (at esophagus)	61.5‡				
Intestine width (max.)	77–100	100			
Anus to post. end	446–477	400–530	400–530	390–440	364–509
Protostom length	15.4–22	15–25			
Protostom width	35.7‡	25–30			
Mesostom length	22–31	25–30			
Mesostom width	17.3‡	20–25			
Excretory pore from ant. end	410‡	350–400			
Nerve ring from ant. end	232‡	250		220–300	270–320
Vulva diameter	46–61	40–50			
Vulva to post. end†	1.23–1.31	1–1.4	1–1.33	0.78–1.07	0.91–1.55
Vagina length†	2				
Vagina width (near uteri)	57.1‡				
Vagina width (near vulva)	36‡	50			
Uteri width	123–146	100			
Ovary width	22–30				

**Oxyspirura parvovum.*

†These measurements in millimeters; all others in microns.

‡Average measurements (10 specimens).

TABLE 2

REPORTED MEASUREMENTS OF ADULT MALE EYEWORMS

MEASUREMENTS	SCHWABE (Oahu, T.H.) 1948–49*	RANSOM (Florida) 1904	SWEET (Australia) 1910†	FIELDING (Australia) 1928†
Length‡	9.2–13	12–14	9.2–14.5	8.2–15.47
Width (ant. end)	75	50		74
Width (max.)	339	200–350	260–330	254–327
Width (at cloaca)	143	65–150		136
Esophagus length‡	1.37			
Esophagus width (post. end)	107			
Intestine width (max.)	111			
Buccal capsule length	53.5			
Excretory pore from ant. end	410			
Nerve ring from ant. end	285			
Cloaca to post. end	285	320–400		253–390
Long spicule length‡	4.15			3.64–4.55
Short spicule length	232			214–235

*Average measurements (10 specimens).

†*Oxyspirura parvovum.*

‡These measurements in millimeters; all others in microns.

FIG. 1. Photomicrograph showing the anterior end of an adult *Oxyspirura mansoni.*

white, thread-like worm attenuated at both the anterior and posterior ends. Adults studied in the laboratory measured from 9 to 17 mm. in length (Tables 1 and 2). The posterior end is more slender and in the male is curved ventrad. The thin, transparent, outer cuticle is smooth; neither transverse nor longitudinal striations were discernible on worms studied. Magalhaes (1888) reported fine transverse striations; these were not apparent to Emmerez and Megnin (1901) or to Ransom (1904).

The following papillae are common to both sexes: a small cervical papilla with a short hair-like process located on each side of the body approximately 440μ from the anterior end; a pair of small latero-caudal papillae near the posterior extremity of the tail; six minute oral papillae; and four large sublateral cephalic amphids. In the male, six pairs of papillae

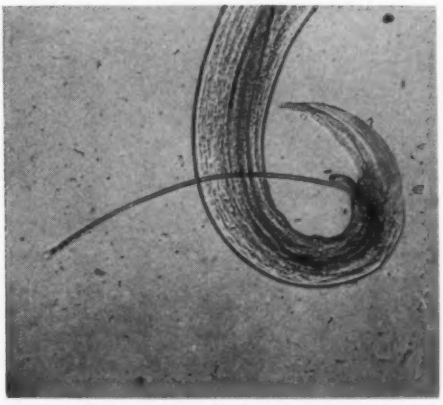

FIG. 2. Photomicrograph showing the posterior end of an adult male *Oxyspirura mansoni.*

surround the cloacal opening, four pairs preanal and two pairs postanal.

The muscle arrangement is of the polymyarian type, with a fan-like arrangement of muscle fibers in the anal region of both the male and the female, attaching the rectum to the dorsal wall.

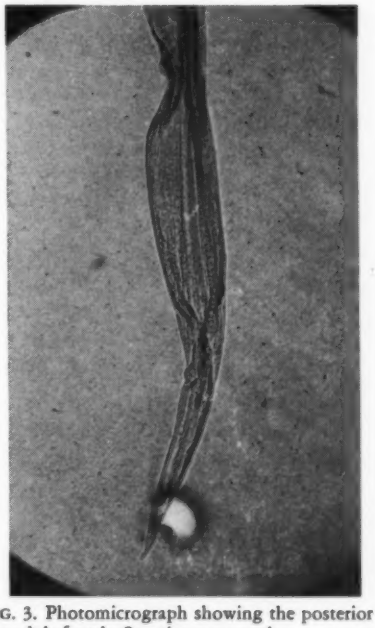

FIG. 3. Photomicrograph showing the posterior end of an adult female *Oxyspirura mansoni.*

FIG. 4. Photomicrograph of median cross section through an adult female eyeworm.

The cuticular buccal capsule is six-lobed and, as is characteristic of the Thelaziidae, is divided into two chambers, the anterior protostom and the posterior mesostom. The esophagus is of the typical spirurid type and is approximately 1.5 mm. in length. It is distinctly divided into a short anterior muscular portion and a posterior glandular portion. The lumen is restricted and triradiate when viewed in cross section. A well-developed esophageal-intestinal valve separates the esophagus from the intestine.

The thin-walled intestine extends almost the entire length of the body, varying only slightly in diameter, and joins the esophagus anteriorly and the rectum posteriorly. The intestinal wall is composed of a single layer of short, ciliated columnar cells. The rectum is thick-walled and muscular and terminates at the ventral anus in the case of the female. In the male, the ejaculatory duct joins the rectum ventrally to form the cloaca.

The excretory system is of the simple H or oxyuroid type. From the ventral pore the common excretory duct extends dorsally through the large excretory cell and divides on the ventral side of the esophagus to join the two lateral excretory canals. These lie embedded in the lateral lines of the body wall. The lateral lines, which extend almost the entire length of the body, are, apparently, each a single large multi-nucleate cell. The lateral canals terminate posteriorly at the laterocaudal papillae.

A nerve ring surrounds the esophagus, cephalic of the excretory pore. In association with it are four large ganglia, two dorsal and two ventral, and a number of smaller cells. A dorsal and a ventral nerve cord extend posteriorly the length of the body, and several smaller nerve fibers extend into the cephalic region.

The mature male possesses two spicules of unequal length, both of which are cuticular in nature, transversely striated, and hollow. The shorter, which is "trough-shaped," measures about 200μ in length by 30μ in maximum width, is only slightly protrusible, and acts primarily as a guide for the longer, more slender spicule. The long spicule is 3 to 4.2 mm. in length by 10μ in maximum width and is capable of being protruded from the cloaca almost its entire length. A short muscular ejaculatory duct extends anteriorly from the cloaca and terminates in a thin-walled seminal vesicle, an uncoiled organ extending over half the length of the body. The single long, coiled testis fills the remainder of the body cavity.

In the female the vulva, which measures 46 to 51μ in diameter, is located ventrally in

FIG. 5. The short, "trough-shaped" spicule of the adult male eyeworm.

the posterior half of the body. It is surrounded by a cuticular ring of highly refractile material. The vagina extends anteriorly from the vulva and is divisible into two parts, by reason of the thickness of the wall. The proximal portion is nearly 150 μ in length and 35 μ in diameter. The distal thicker-walled portion is approximately 60 μ in diameter. The vagina branches to form the two thin-walled uteri. These extend forward to the posterior region of the esophagus, where they reflex and extend back to the region of the vulva. The diameter of the uteri decreases to 22–30 μ to form the two ovaries which lie as a coiled mass in the posterior portion of the body cavity.

HOSTS OF THE EYEWORM

Nematodes inhabiting the eyes of birds have been reported from a number of species. Most of these parasites are members of the genera *Thelazia* and *Ceratospira*, or are species of the genus *Oxyspirura* other than *O. mansoni*.

The hosts of only those eyeworms which have been definitely identified as *Oxyspirura mansoni* (or *parvovum*) are recorded here.

Definitive hosts

Manson's eyeworm has been reported to occur naturally in the following birds: domestic chicken (*Gallus domesticus*) (Cobbold, 1880); turkey (*Meleagris gallopava*) (Cram, 1927); peafowl (*Pavo cristatus*) (Magalhaes, 1888); English sparrow (*Passer domesticus*) (Illingworth, 1931; Alicata, 1947); mynah bird (*Acridotheris tristis*) (Alicata, 1947); Chinese dove (*Streptopelia chinensis*) (Alicata, 1947; Schwartz and Schwartz, 1949); Japanese quail (*Coturnix coturnix japonica*) (Schwartz and Schwartz, 1949); pheasant (*Phasianus torquatus torquatus* and *P. vesicolor vesicolor*) (Schwartz and Schwartz, 1949).

Through the cooperation of Paul Breese, Director, the birds in the Honolulu Zoo are being examined for the presence of *Oxyspirura mansoni*. This survey is not complete as yet, but the following new hosts may be recorded: the great Argus pheasant (*Argusianus argus argus*) and the Siamese fireback pheasant (*Diardigallus diardi*).

Role of the natural reservoir hosts in the spread of the parasite in Hawaii

During the course of this investigation mynah birds, English sparrows, and Chinese doves have been trapped on the University campus and have been found to harbor Manson's eyeworm. Similar observations have been made by other investigators in other parts of Hawaii (Illingworth, 1931; Alicata, 1947; Schwartz and Schwartz, 1949; Tanada, personal communication).

TABLE 3
NUMBERS OF INFECTIVE LARVAE PER ROACH
(100 SURINAM ROACHES EXAMINED AT EACH LOCALITY)

STAGE	RANGE	MIYATA POULTRY FARM, WAIALAE, OAHU	UNIVERSITY FARM, MANOA VALLEY, OAHU*	WAIKIKI, OAHU†
Adult roaches	Max.	36	3	None
	Min.	16	0	
	Ave.	23		
Nymphs (Final instar)	Max.	34	2	None
	Min.	1	0	
	Ave.	3		
Young nymphs	Max.	6	0	None
	Min.	0	0	

*Roach population low (daily removal of manure, weekly chlordan spray).
†Approximately 4 miles from nearest poultry farm.

Since these commonly infected birds are widespread and numerous throughout the Hawaiian Islands, it seemed desirable to ascertain the role they play in the dissemination of the parasite. To determine this, the degree of infestation of Surinam roaches was established at (1) a heavily infested poultry farm in Waialae, Honolulu, Oahu; (2) a relatively clean poultry yard in Manoa Valley, Honolulu; and (3) a residential area in Waikiki, Honolulu. In all three places roaches were numerous.

As shown in Table 3 the roaches from (1) harbored a large number of infective eyeworm larvae per roach. At (2), where low infestation of the chickens resulted from strict sanitation and frequent removal of the manure, but where large numbers of wild birds gathered to feed, the number of larvae per roach was very low. At (3), an area at some distance from any poultry farm, but where wild birds were also very numerous, no larvae were found in the many roaches examined.

Inasmuch as domestic fowl and wild birds are the only sources of infection of the local roaches these data indicate that the local wild birds are of little importance as reservoir hosts in the dissemination of the eyeworm population. Apparently their feces are too scattered to be eaten to any great extent by the roaches.

Mammals as hosts of Manson's eyeworm

In no case has *Oxyspirura mansoni* been known to occur naturally in the eyes of a mammal. Fielding (1927) found that infective eyeworm larvae placed in the eyes of guinea pigs would develop to maturity.

To check Fielding's observations on another mammal, I obtained several white rats. Each of these was forcibly fed four infected roaches. The next day the eyes were anesthetized with a 5 per cent solution of butyn and examined carefully for eyeworm larvae. No larvae were found.

Approximately 30 infective larvae were then introduced by pipette into the mouth of one of the rats. On examination of the eyes 24 hours later, no larvae were found.

Two rats then received approximately five eyeworm larvae per eye. One was examined after 10 days and larvae were seen in both eyes. The rat was necropsied and the worms were removed. They had molted to the fourth stage and the reproductive organs were developing normally. The second rat was killed 25 days after the larvae were placed in its eyes. Adult male and female worms were recovered from both eyes.

LIFE HISTORY OF THE PARASITE

Apparently little effort had been made before about 1927 to ascertain the life cycle of *Oxyspirura mansoni*. Previously Emmerez and Megnin (1901), and Emmerez (1918), Ransom (1904), and Ozoux (1910) had attempted to transmit the infection directly from one chicken to another with embryonated eggs and/or first-stage larvae; but they carried the work no further when their efforts were unsuccessful.

Kobayashi (1927) in Formosa and Sanders (1928) in Florida found that an intermediate host, which they identified as the cockroach *Pycnoscelus surinamensis* Linn., was essential for the completion of the life cycle of the parasite. Previously Fielding (1926) had shown the same roach to be the intermediate host of the Australian eyeworm of poultry, *Oxyspirura parvovum* Sweet. Fielding (1927 and 1928*a*) studied the developmental anatomy of the Australian eyeworm, but because of his uncertainty as to whether the species was *O. mansoni* or *O. parvovum*, he referred to it simply as the eyeworm of poultry in his latter paper. The validity of *O. parvovum* as a species was questioned by Tryon (1926). This lack of clarity as to species, together with the fact that Fielding's drawings were not identifiable with the material found in Hawaii, led me to investigate the life history of Manson's eyeworm under Hawaiian conditions.

Life cycle in general

The eggs of the parasite are laid by the

FIG. 6. Photomicrograph of the vagina of a gravid female eyeworm showing embryonated eggs.

adult females in the eyes of the definitive host. They are washed down the naso-lacrimal ducts with the eye fluid into the mouth, swallowed, and finally passed out with the excrement. The intermediate host is infected by eating embryonated eggs or first-stage larvae in the feces of infected birds. After a developmental period of approximately 51 days in the roach, the larvae are infective to the definitive host. They gain entrance when the host roach is consumed by a suitable bird. The larvae seldom pass farther than the crop of the definitive host (Fielding, 1926), where they migrate from the tissues of the roach under stimulation of heat and moisture.

The infective larvae then crawl up the esophagus, reach the roof of the mouth, and gain entrance to the eyes through the naso-lacrimal ducts. During this study worms have been observed in the eyes of a chicken within 5 minutes after the ingestion of an infected roach.

The eyeworm eggs

During the course of this study several attempts were made to recover embryonated eggs from the eyes of infected birds. Fluid was removed from the eye with a pipette and examined beneath the microscope, but in no case were eggs observed. However, they were recovered in varying quantities from the crop, intestinal contents, and feces of infected birds. The eggs were elliptical in shape, had a shell thickness of 1 to 1.5 μ, and were approximately the same size as those measured in the

TABLE 4

REPORTED MEASUREMENTS OF EYEWORM EGGS (ALL MEASUREMENTS IN MICRONS)

STAGE	RANGE	SCHWABE (Oahu, T.H.) 1948–49	RANSOM (Florida) 1904	SWEET (Australia) 1910*	FIELDING (Australia) 1928†	FIELDING (Australia) 1928*
Embryonated eggs from feces	Max.	60x45				
	Min.	42x23				
	Ave.	53x40				
Embryonated eggs from vagina and uteri	Max.	50x28.5	65x45	45x30		
	Min.	35.7x17.8	50x40	33x25		
	Ave.	41.6x23.7			43x31	41x30
Shelled, segmented eggs from uteri	Max.	42.9x32				
	Min.	28.4x14.3				
	Ave.	36.7x22.9				
Unshelled, non-segmented eggs from uteri	Max.	28.25x10.7				28x14
	Min.	21.6x7.2				24x12
	Ave.	23.4x9.5	24x12			

**O. parvovum.*
†Old fixed *O. mansoni* eggs.

vagina of gravid female worms (Table 4). The shell had a smooth surface with no discernible markings.

Ransom (1904) obtained embryonated eggs from the uteri of gravid worms. These were placed in "salt solution" and were reported to have hatched in 3 days. The larvae obtained were dead, or were feeble and soon died. Sanders (1928) employed a similar technique, substituting distilled water for the saline solution, and found that embryonated eggs from gravid females hatched in 3 days.

Fielding (1927) succeeded in hatching living larvae in the following media: 0.9 per cent NaCl, 1.4 per cent NaCl, other physiological solutions, 1 per cent citrated fowl blood, moistened earth, fowl feces (plus sand and saline), sterile fowl feces (plus saline and charcoal), moistened bread. Hutson (1943) was unsuccessful in hatching eggs in distilled water but obtained living first-stage larvae from cultures of distilled water plus fowl feces. Upon introduction into the body cavity of a roach these larvae developed normally.

It seemed desirable to determine, if possible, whether eyeworm eggs hatch more readily in the digestive tract of the intermediate host or in fowl feces. Attempts were made to obtain mature eggs from the crops of infected chickens. (Some embryonated eggs obtained from the uteri of gravid worms may not be fully matured. Such eggs in other species of nematodes have been known to "hatch" abnormally in artificial media.) Although eggs were usually present in the crop, they could not be separated in sufficient quantity for the experiment. This made it necessary to obtain embryonated eggs from macerated female worms. To avoid as far as possible the selection of immature eggs, special care was taken to collect by use of a fine pipette only the largest eggs.

These were placed in three dishes containing (1) physiological saline solution, (2) physiological saline solution plus sterilized fowl feces, and (3) physiological saline solution plus the macerated alimentary tracts of several Surinam roaches. None of the eggs had hatched by the end of the second day, but quiescent or feeble larvae were observed in each of the three cultures on the third day. None of the larvae survived. Although additional work is indicated, apparently, under the conditions of this experiment, the medium had no appreciable effect upon the rapidity with which eyeworm eggs hatched.

Larvae observed both in the artificial media and in the alimentary tract of the intermediate host apparently hatched in the following manner. (The terminology used is based on the description of the spirurid egg by Christenson in Chitwood *et al.*, 1940.) The chitinous middle layer of the shell separated from the inner vitelline membrane at either or both poles. The region of the poles then became thinner, producing polar operculations marked by ill-defined sub-terminal lines of fracture. One or both caps either broke off at the line of fracture or dissolved, leaving a barrel-shaped shell, open at either or both ends. The embryo then freed itself from the thin vitelline membrane and squeezed through the polar opening.

Similar observations have been made by Ransom (1904), Sanders (1928), and Fielding (1927).

Development in the intermediate host

Eggs were obtained from gravid female worms and were fed to young laboratory-raised roach nymphs. One nymph was dissected 24 hours after feeding, and numerous embryonated and non-embryonated eggs were found in the crop. No eggs or egg shells were found in the feces of the nymphs examined at this time.

At 48 hours, several first-stage larvae were found free in the lumen of the crop and anterior midgut, and many others were observed in the process of hatching. The empty shells were barrel-shaped, which suggested that they hatched by splitting off one or both polar caps, as previously described. Several of the larvae were rather firmly attached to cellular

debris by the tip of the tail. Embryonated eggs were found in the midgut until the seventh day, and numerous larvae were present until the ninth day. A single larva was found in the midgut on the eighteenth day. It was almost double the size of those seen there previously.

First-stage larvae were observed for the first time in the body cavity on the eighth day, and by the tenth day many were seen. Some were wandering freely in the cavity, but most were found in the adipose tissue lining the abdominal wall. Apparently they migrated through the wall of the midgut, and after wandering in the body cavity for a short time, burrowed into the abdominal fat. The larvae became lethargic at this stage and were extremely difficult to extricate. They grew only slightly in length, broadened considerably, lost their long, pointed tails, and assumed a more-or-less club-shaped appearance because of the enlargement of the several large rectal cells.

Incomplete encystment actually occurred in this stage in some instances, with the ill-defined cyst measuring approximately 0.3 mm. by 0.5 mm. Thereafter little change took place until about the seventeenth day when larvae measuring 250μ to 320μ in length and with the cuticular sheath loosened at both the anterior and posterior ends were observed. Larvae in this pre-molting condition were seen until the twenty-fifth day, at which time a second-stage larva which measured 990μ in length was observed.

Complete encystment occurred in the second stage of larval development. The cysts were nearly spherical in shape and measured approximately 0.8 mm. by 0.8 mm. They were found attached to the alimentary tract, particularly around the rectum and entangled in the Malpighian tubules. The cysts were thin-walled and transparent. The wall, apparently of loose connective tissue, consisted of a gelatinous matrix and a few scattered cells. The wall was richly tracheated, which constituted evidence that the cyst was formed by the cockroach and not secreted by the parasite. The cysts were filled with fluid and the coiled larvae were able to move about freely in them.

On the thirty-third day encysted second-stage larvae measuring 1.8 mm. to 1.85 mm. were observed; those on the fortieth day had attained a length of 2.6 mm. to 4.5 mm. On the forty-fifth day a second-stage larva 6.62 mm. in length was observed in the process of molting. Ecdysis evidently takes place between the forty-fifth and fiftieth days, at which time the last molting larvae were seen.

Many of the parasites were able to free themselves from their cysts through their increased activity during the period of ecdysis, and on the fifty-first day numerous third-stage larvae were found, some encysted, but most wandering freely in the body cavity. These early third-stage larvae measured from 7.4 mm. to 8.3 mm. in length and were extremely active.

Whether or not those larvae which were unable to free themselves during the molting period eventually escape from the cyst could not be ascertained.

Upon the attainment of the third stage, the larvae were infective to the definitive host, as was shown by their appearance in the eyes of chickens within 5 minutes after they were introduced into the mouth by pipette.

Development in the definitive host

Large numbers of infective larvae were obtained from roaches by use of the Baermann apparatus. They were introduced by pipette into the mouths of 4-week-old chicks. The larvae migrated up the naso-lacrimal ducts and were observed to enter the eyes several minutes after they were introduced. Chicks were killed every 2 days, and the worms were removed from the eyes and examined microscopically.

On the second day the larvae appeared much the same as they did in the cockroach. On the fourth day several third-stage larvae in the process of molting were observed.

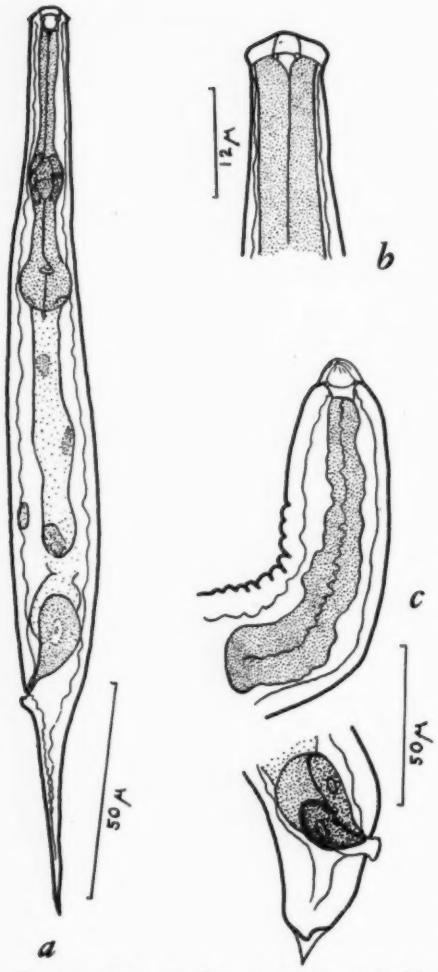

FIG. 7. *a*, First-stage larva; *b*, anterior end of late first-stage larva, *c*, first-stage larva in process of molting, showing loosened cuticle at anterior and posterior ends.

Fourth-stage larvae were first seen on the fifth day, although some third-stage larvae were still present until the seventh day. The reproductive organs developed rapidly during this period: the vulva of the female was apparent on the seventh day and the developing short spicule of the male on the ninth day.

A separate mesostom and protostom had begun to form by the thirteenth day. For most larvae the final molt occurred about the twenty-first day, and young adults were present on the twenty-third day. Embryonated eggs were first observed in the crop contents of a chicken on the thirty-second day. Egg laying apparently began between the thirtieth day, when the previous negative examination was made, and the thirty-second day.

DESCRIPTION OF THE LARVAL STAGES

First-stage larvae

Because of their small size and poor development the various structures of the first-stage larvae were discerned only with difficulty. The newly hatched larvae were long and slender, being somewhat attenuated at the anterior and posterior ends. The anterior end was rather blunt and the relatively long tail was acute. In the later period of this stage, the tail shortened considerably, the relative growth in width exceeded the growth in length, and the body assumed a more-or-less club-shaped appearance because of the enlargement of the several large rectal cells. The maximum size observed in this stage was a length of 339μ and a width of 24.9μ. (See Table 5. Tables 5, 6, 7, and 8 show detailed measurements of a single typical larva for each of the days recorded. When size variations among the larvae on a particular day were significant, detailed measurements of more than one larva are given. When the sex of the larvae could be readily determined, measurements of both male and female larvae for a particular day were made.)

The cuticle was very thin and transparent and bore fine transverse striations. No papillae were apparent in this stage.

The oral opening was surrounded by a ring of highly refractile material. The transparent esophagus extended approximately one-third the length of the body and terminated as a large spherical bulb, possessing what appeared to be an esophageal valve. The intestine consisted of a number of rather large, ill-defined cells containing numerous large vacuoles of lipid-like material. The ventral anal

TABLE 5
MEASUREMENTS OF FIRST-STAGE LARVAE (ALL MEASUREMENTS IN MICRONS)

MEASUREMENTS	DAYS AFTER INFECTION				
	3	5	8	17	18
Length	125	174	207	249	286
Width (ant. end)		7	7	7.5	7
Esophagus length		57.1		107	93
Anus to post. end		49.9	46.4	39.2	32.2
Width (max.)	14.3	17.8	17.8	32	18

aperture was often seen with a posterior cuticular fold partially covering it, and a few large rectal cells (apparently three in number) were well developed.

A nerve ring was seen encircling the esophagus at approximately two-thirds of the distance from its anterior end.

Neither an excretory pore nor an excretory cell was apparent in this stage.

A minute genital primordium, approximately 75 μ from the posterior end, was visible on the ventral body wall in several living specimens.

Second-stage larvae

Rapid growth occurred during this stage of larval development. The length increased from 990 μ in early second-stage larvae to 6.62 mm. in the latter portion of the stage. The larvae were long and slender with tapering tails, on the end of which four small papillae were discernible in the later part of the stage.

The cuticle was relatively thin and bore marked transverse striations. A provisional buccal capsule had begun to form, but no cephalic papillae were visible.

The esophagus was long and slender and in the late second stage extended approximately one-half the length of the body in some larvae. Two gland-like structures were apparent at its anterior end, and the esophageal-intestinal valve was well formed.

The intestine was a well-defined, thin-walled tube, varying only slightly in diameter and extending from the esophagus to the rectum. The cellular structure of its wall was apparent.

There were three large rectal cells and several smaller ones immediately anterior to the anus, which was located ventrally approximately 170–190 μ from the posterior end.

TABLE 6
MEASUREMENTS OF SECOND-STAGE LARVAE

MEASUREMENTS	DAYS AFTER INFECTION				
	27	33	40	40	45
Length	999.6	1.85*	2.6*	4.5*	6.62*
Width (ant. end)	54	53.5	38.5	62	52
Width (middle)	67.8	89	107.8	170	172
Width at anus		24	92.4	77	85
Esophagus length		357	400	616	749
Esophagus width (post. end)				43	
Anus to post. end	53.5	160	170	246	250
Excretory pore to ant. end		178		250	360.5
Nerve ring to ant. end		89		160	185.6
Intestine width			62	112	
Genital primordia to post. end				890	

*These measurements in millimeters; all others in microns.

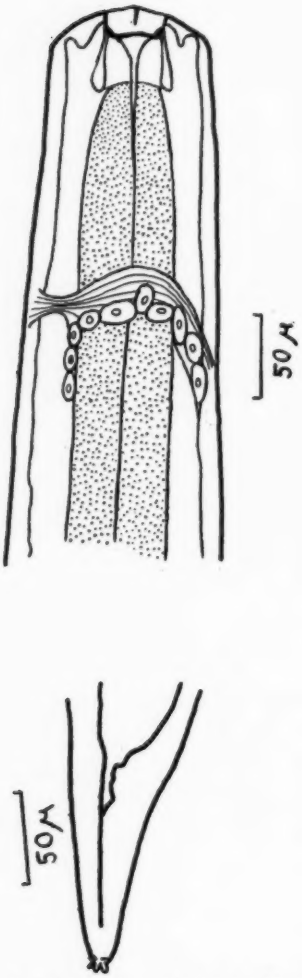

FIG. 8. Anterior and posterior ends of late second-stage larva.

An excretory pore and a large excretory cell were plainly visible on the ventral side of the esophagus, 250–300 μ from the anterior end.

The nerve ring and several small ganglion cells encircled the esophagus, about 100 μ anterior to the excretory pore.

The genital primordium was visible in the living larvae ventrad of the intestine, approximately 500 μ from the anus.

Third-stage larvae

Third-stage larvae varied from 7.53 mm. to 8.31 mm. in length and had a maximum width of approximately 157 μ. Other than in this feature, their over-all appearance was much the same as that of the second-stage larvae.

The cuticle was smooth and no striations were discernible, either transverse or longitudinal. The anterior oral opening was six-lobed, and four sublateral papillae were plainly visible projecting at right angles to the surface. No caudal papillae were present in this stage.

The esophageal gland-like structures apparent in the second stage were not discernible in the third-stage larvae, but a number of cells were seen to surround the esophagus at its anterior end. The esophagus was distinctly divided into an anterior muscular portion having a length of about 210 μ and a posterior glandular portion approximately 600 μ in length. The remainder of the alimentary tract appeared much the same as that of the second-stage larvae.

TABLE 7

MEASUREMENTS OF THIRD-STAGE LARVAE*

Days after infection	51*
Length†	7.53–8.31
Width (ant. end)	53.5
Width (max.)	157
Width (at anus)	92.3
Buccal capsule length	35.7
Esophagus length	846
Esophagus width (post. end)	71.5
Intestine width (max.)	107
Nerve ring from ant. end	178.5
Excretory pore from ant. end	303
Anus to post. end	184

*In intermediate host. For measurements of third-stage in definitive host, see Table 7.

†This measurement in millimeters; all others in microns.

In addition to the excretory pore and cell apparent in the second stage, two lateral excretory canals were traced from the region anterior of the excretory pore to very near the tip of the tail. Each canal sent off an anterior branch which joined ventrad of the esophagus and entered the excretory cell as a common excretory duct. The lateral canals

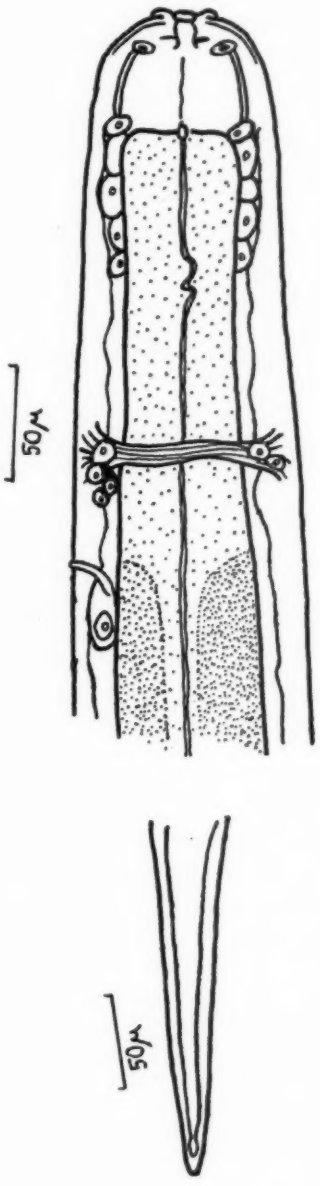

FIG. 9. Anterior and posterior ends of third-stage larva.

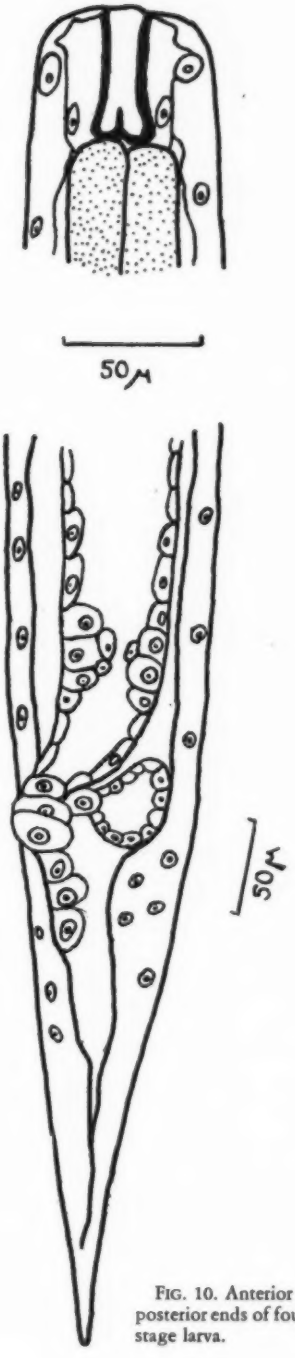

FIG. 10. Anterior and posterior ends of fourth-stage larva.

TABLE 8

MEASUREMENTS OF THIRD- AND FOURTH-STAGE LARVAE IN THE DEFINITIVE HOST

MEASUREMENTS	DAYS AFTER INFECTION														
	THIRD STAGE		FOURTH STAGE												
	2	4	5	5	7	9	11	11	13	16	18	18	21	21	23
	—	—	♀	♂	♀	♀	♀	♂	♀	♂	♀	♂	♀	♀	♀
Length*	8.23	10.38	10.38	10	12.08	10.1	10.3	9.7	12.1	11.4	12.6	10.4	12.3	14	12.8
Width (middle)	257	250	222	176	250	214	303	267	267	326	307	284	293	290	310
Width at vulva							176		183		185		204	196.5	196
Width at anus	89.4	87	89.4	92.8	100	87	92.8	103	104	100	100	110	100	92.8	92.8
Oral opening width	35.7	35.7	32	32	35.7	40	32	28.6	32	35.7	24	21.4	21.4	28.6	35.7
Buccal capsule length	42.9	54	42.9	50	47	50	50	42.9	47	42.9	45	40	57.2	57.2	35.7
Esophagus length (ant. portion)		340	250	330	330	287	267	330	287	267	250	267	293	304	271
Esophagus length (total)	930	1,285	1,039	1,150	1,212	1,032	1,140	1,080	1,230	1,060	1,039	1,140	1,220	1,230	1,054
Esophagus width (post. end)	62	77	85	100	92.8	92.8	85	85	92.8	100	92.8	92.8	96.5	92.8	103.5
Nerve ring to ant. end	250	268	214	287	287	234	228	275	234	172	226	214	222	279	214
Excretory pore to ant. end	357	392	303	303	392	303	326	360	357	330	342	307	357	379	307
Intestinal width (max.)	89.4	71.4	89.4	77	77	75	96	96	81	73	54	68	74	71	71.4
Vulva to post. end.					1,130	850	784		950		950		910	883	1,000
Anus to post. end.	340	357	340	392	430	330	357	392	370	330	370	340	340	360	392

*These measurements in millimeters; all others in microns.

were each embedded in a multinucleate lateral line 50 μ in width.

The nervous system appeared much the same as in the second-stage larvae.

The sexes could be distinguished readily in the third stage. In the female the genital primordium could be seen attached to the ventral body wall approximately 650 μ from the posterior end. In the male the primordium was similarly situated but unattached. The primordium in both sexes measured approximately 35 μ by 14 μ in this stage and was composed of several cells.

Fourth-stage larvae

In general proportions the fourth-stage larvae differed little in appearance from those of the third stage. Early fourth-stage larvae measured about 10 mm. in length while those in the later portion of the stage measured from 12.8 to 14 mm.

Fine transverse striations were evident in the transparent cuticle. The four sublateral papillae each measured approximately 4.6 μ in length. In addition, by the twenty-first day, the two latero-caudal papillae had begun to form, and the preanal and postanal papillae of the males were evident.

By the thirteenth day the separate protostom and mesostom could be differentiated, and in the later part of the stage the buccal capsule appeared much the same as in the adult.

The remainder of the alimentary tract showed little change from that of the third-stage larvae, the intestine being displaced somewhat to allow room for the developing reproductive organs.

The lateral excretory canals were seen to terminate in the latero-caudal papillae in the late fourth-stage larvae. Other than this, the excretory system had apparently achieved its full development by the end of the third stage.

The only additional development noted in the nervous system in the fourth stage was the appearance of two large dorsal and two large ventral ganglion cells near the nerve ring.

In the fourth-stage larvae the greatest development occurred in the reproductive system. By the fourth day the genital primordium in both sexes measured approximately 214 μ in length and in the case of the female was attached to the ventral body wall. The point of attachment, which later became the vulva, was approximately 894 μ from the posterior end. In the male the genital primordium became a U-shaped tube with two terminal bulbous growing tips developing toward the posterior end. By the ninth day the short spicule of the male had begun to form and the vulva of the female was apparent, although it remained closed externally during the entire fourth stage. The reproductive tract, at least in the female, appeared almost complete by the thirteenth day. By the sixteenth day the long spicule of the male could be recognized. The male reproductive system was well formed by the twenty-first day; the ejaculatory duct could be seen to enter the ventral side of the rectum at its posterior terminus, the anal papillae were evident, and both spicules were well developed.

Acknowledgments: I wish to express my sincere appreciation to Dr. J. E. Alicata, Parasitologist, Hawaii Agricultural Experiment Station, for suggesting the original problem and making certain facilities of the Department of Parasitology available to me; Mr. Paul Breese, Director of the Honolulu Zoo, for examining and permitting the examination of birds in the Honolulu Zoo; Dr. R. W. Hiatt, Chairman of the Department of Zoology and Entomology, University of Hawaii, for providing such excellent facilities for my work; Mr. Hiromu Matsumoto, Junior Chemist, Hawaii Agricultural Experiment Station, for the white rats utilized in this work; Mr. Harry Miyata, Miyata Poultry Farm, for permitting the unrestricted use of his flocks and farm; and Dr. M. M. Rosenberg, Associate

Poultry Husbandman, Hawaii Agricultural Experiment Station, for providing the experimental chickens employed in this study.

REFERENCES

ALICATA, J. E. 1947. Parasites and parasitic diseases of domestic animals in the Hawaiian Islands. *Pacific Sci.* 1(2): 69–84.

ALMEIDA,[?]. 1933. *Arch. Esc. Sup. Agr. e Med. Vet.* 10: 171. (*Fide* Reis, J., P. Nobrega, and A. S. Reis. 1936. *Tratado De Doencas Das Aves.* 327–328. Sao Paulo, Brazil.) [In Portuguese.]

CHITWOOD, B. C., *et al.* 1940. *An introduction to nematology.* Sect. I, Pt. III, and Sect. II, Pt. I: 125–240. M. B. Chitwood, Babylon, N. Y.

COBBOLD, T. S. 1880. (Prefatory note to P. Manson, "Further observations on microfilariae, with description of a new species.") *Quekett Micros. Club, Jour.* 6(44): 130–132.

CRAM, E. B. 1927. Bird parasites of the nematode suborders Strongylata. Ascaridata and Spirurata. *U. S. Natl. Mus., Bul.* 140: 311–328.

DODD, S. 1909. Eyeworms of poultry. *Queensland Dept. Agr., Rpt.* 1–100. (*Fide* Fielding, 1926.)

EMMEREZ, C. 1918. *Poultry in Mauritius.* Mauritius Dept. Agr., Bul. 12. (*Fide* Fielding, 1926.)

——— and P. MEGNIN. 1901. Un nouveau parasite et une nouvelle maladie chez les poulets de l'ile Maurice. [*Paris*] *Soc. de Biol. Compt. Rend.* 53(33): 933–935. (*Fide* Ransom, 1904.)

FIELDING, J. W. 1926. Preliminary note on the transmission of the eyeworm of Australian poultry. *Austral. Expt. Biol. and Med. Sci., Jour.* 3: 225–232.

——— 1927. Further observations on the life history of the eyeworm of poultry. *Austral. Expt. Biol. and Med. Sci., Jour.* 4: 273–281.

——— 1928*a*. Additional observations on the development of the eyeworm of poultry. *Austral. Expt. Biol. and Med. Sci., Jour.* 5: 1–8.

——— 1928*b*. Observations on eyeworms of birds. *Queensland Agr. Jour.* July, 1928.

HUTSON, L. R. 1943. *Miscellaneous veterinary research in Antigua, B. W. I. Studies on Manson's eyeworm of poultry.* 1–32. (Unpublished thesis: University of Toronto.)

ILLINGWORTH, J. F. 1931. Manson's eyeworm distributed by English sparrows. *Hawaii. Ent. Soc., Proc.* 7: 461.

KOBAYASHI, H. 1927. On the life history of the *Oxyspirura mansoni* and pathological changes in the conjunctiva and ductus lacrymalis caused by the worm. *Jap. Path. Soc., Trans.* 17: 239–242.

DE MAGALHAES, P. S. 1888. Notas helminthologicas. *Brazil. Soc. de Med., Rev.* 1(1): 5–20. (*Fide* Ransom, 1904.)

OZOUX, M. 1910. La filaire de l'oeil du dindon. [*Paris*] *Soc. de Biol., Compt. Rend.* 1: 974–975.

PICARD, W. K. 1929. In:Ned. Indie voorkomende Pluimveezieten. [English summary.] *Nederland. Indische Bl. v. Diergeneesk.* 41(1): 42–48.

RANSOM, B. H. 1904. *Manson's eyeworm of chickens with a general review of nematodes parasitic in the eyes of birds.* U. S. Dept. Agr., Bur. Anim. Indus., Bul. 60: 1–54.

SANDERS, D. A. 1928. Manson's eyeworm of poultry. *Amer. Vet. Med. Assoc., Jour.* 25(5): 568–584.

——— 1929. *Manson's eyeworm of poultry.* Fla. Agr. Expt. Sta., Bul. 206.

SCHWABE, C. W. 1949. Observations on the life history of *Pycnoscelus surinamensis* Linn., the intermediate host of the chicken eyeworm in Hawaii. *Hawaii. Ent. Soc., Proc.* 13(3): 433–436.

——— 1950*a*. Studies on *Oxyspirura mansoni*, the tropical eyeworm of poultry. III. Preliminary observations on eyeworm pathogenicity. *Amer. Jour. Vet. Res.* 11(40): 286–290.

——— 1950*b*. Studies on *Oxyspirura mansoni*, the tropical eyeworm of poultry. IV. Methods for control. *Hawaii. Ent. Soc., Proc.* 14(1): 175–183.

SCHWARTZ, C. W., and E. R. SCHWARTZ. 1949. *The game birds in Hawaii.* 168 pp. Hawaii Board of Commissioners of Agriculture and Forestry, Honolulu, T. H.

TRYON, H. 1926. [Validity of *O. parvovum.*] *Queensland, Agr. Gaz.* 25 (1926): 272. (*Fide* Fielding, 1926.)

WILCOX, E. V., and C. K. MCCLELLAND. 1913. Eyeworm of chickens. *Hawaii Agr. Expt. Sta., Press Bul.* 43: 1–14.

Viability of Hawaiian Forest Tree Seeds in Storage at Various Temperatures and Relative Humidities[1]

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INTRODUCTION

IN HAWAII the Territorial Board of Commissioners of Agriculture and Forestry is charged with the maintenance of forest reserves. Before World War II forest tree seeds were imported from outside sources for reforestation purposes. During the war years, when seeds could not normally be imported because of the critical shipping situation, it was realized that some locally harvested tree seeds could not be kept under ordinary conditions for any extended period without impairment of their viability.

At the request of the Territorial Board of Commissioners of Agriculture and Forestry, studies on the viability of forest tree seeds were pursued at the University of Hawaii Agricultural Experiment Station between the years 1944 and 1948. Seeds of the following trees were tested: paper bark (*Melaleuca Leucadendron* Linn.), brush box (*Tristania conferta* R. Br.), turpentine tree (*Syncarpia laurifolia* Ten.), Norfolk Island pine (*Araucaria excelsa* R. Br.), mamani (*Sophora chrysophylla* Seem.), Monterey cypress (*Cupressus macrocarpa* Hartw.), and Indian sandalwood (*Santalum album* Linn.). It is the purpose of this paper to present the results of experiments designed to develop practical means of prolonging the viability of seeds of these forest trees under storage.

It had previously been found that because the prevailing temperatures and relative humidities of the atmosphere in Hawaii are generally high, seeds of garden, field, and forage crops in ordinary storage deteriorated rapidly (Akamine, 1943). It was further determined that, in order to maintain their longevity, seeds should be stored in a medium in which either the temperature or the relative humidity is kept below that of the atmosphere, or, better still, in a medium in which both the temperature and the relative humidity are kept below those of the air.

Germination and viability studies conducted on forest tree seeds have not been as extensive as those conducted on seeds of other species. Cold storage prolonged the life of Noble fir seed (Isaac, 1934). Moss (1938) found that seeds of three species of *Populus* produced a germination of 70 per cent after a storage period of 2 years under calcium chloride at 23° F. These seeds lost their viability in 2 to 4 weeks when they were stored at room temperature (70° F.). Coniferous seeds have been successfully stored for several years in sealed containers at 36° to 40° F., provided the moisture content of the seeds did not exceed 5 to 8 per cent (Heit and Eliason, 1940; Latour, 1942). The literature on viability studies of forest tree seeds has been reviewed by Toumey and Korstian (1931: 109–152) and by Baldwin (1942: 81–94). More recently Crocker (1948: 28–66) and Porter (1949) also reviewed the work on storage studies of seeds, including those of forest trees.

[1]Published with the approval of the Director of the University of Hawaii Agricultural Experiment Station as Technical Paper 213. Manuscript received March 23, 1950.

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EXPERIMENTAL PROCEDURE

The seeds of the seven forest tree species used in these studies were harvested and collected from the various forest reserves throughout the Territory by the foresters of the Territorial Board of Commissioners of Agriculture and Forestry. The viability studies were conducted by the Department of Plant Physiology at the University of Hawaii Agricultural Experiment Station. Freshly harvested and cured seeds were used. Species and their storage periods are listed in Table 1.

Because of the difficulty encountered in most of the species in separating normal embryonated seed from empty seed by external appearance the "per cent normal seed" for each species was determined from internal examination of lots of known numbers of seeds obtained at random (Table 1). Germination tests were conducted on lots of seed counted out at random, and the percentage of germination was based on the "per cent normal seed."

Seeds were stored at relative humidities of approximately 30, 45, 60, 75, and 90 per cent at temperatures of 45°, 59°, and 70°–80° F. (room temperature).[3] The required humidities were maintained with solutions of sulphuric acid of various concentrations (Akamine, 1943) in large desiccators. Some seeds of each species were stored in airtight containers without humidity control at each temperature, and control lots of seeds stored in the open were also included under each temperature. At intervals during the storage period, the specific gravity of the sulphuric acid solutions was determined with a hydrometer, and any divergence from the required specific gravity was corrected by the addition of water or concentrated sulphuric acid.

At the time of storage, an initial germination test was conducted on the seeds of each species. Thereafter, germination tests were conducted at intervals, once in approximately 1 to 2 months, at the beginning of the storage period, and once in approximately 6 months, during the latter part. Data on the germination test period, germination condition, number of replications, and number of seeds per replication for seeds of each species are shown in Table 1. In all cases, tap water was used in the substratum. The sandalwood seed, with its seedcoat removed by hand, was treated with a fungicide ("Thiosan"). The seedcoat was removed to hasten germination, and the fungicide was applied to prevent the contamination of the germination medium by mold organisms. Before testing them, the seeds of mamani were mechanically scarified for 2 to 3 minutes in a shaking machine (Akamine, 1942), using an equal amount of black sand and seed. The black sand was used to abrade the seedcoat, which in this seed is impervious to water and hence requires scarification in order for the seed to germinate. The few hard unswollen seeds remaining at the end of the germination test were nicked on the seedcoat with a knife and left for an additional period to germinate. In all cases, all sound ungerminated seeds left at the end of the test were considered viable and included in calculation of the germination percentage. Because of their enormous size, the seeds of Norfolk Island pine were germinated in a Minnesota seed germinator at room temperature instead of in the petri dish. The criterion of germination was the emergence of normal primary roots and shoots.

EXPERIMENTAL RESULTS

For the sake of brevity, the voluminous germination data on the stored seeds have been omitted in this paper, and, in their place, graphs[4] constructed from these data are presented in Figures 1 to 7. To present the trend of the germination more readily, the curves for these graphs were drawn from points ob-

[3]The cold storage facilities of the United States Department of Agriculture Bureau of Entomology and Plant Quarantine at Honolulu, T. H., were used during the early stages of this study.

[4]The author is indebted to Herbert Sakamoto for the construction of the graphs.

TABLE 1
DATA ON STORED SEEDS OF FOREST TREE SPECIES

COMMON NAME	SCIENTIFIC NAME	STORAGE		NORMAL SEED	GERMINATION TEST			
		STARTED	CONCLUDED		TEST PERIOD	GERMINATION CONDITION*	NO. OF REPLICATIONS	NO. OF SEEDS PER REPLICATION
				per cent	*weeks*			
Paper bark	*Melaleuca Leucadendron* Linn.	May 5, 1944	May 5, 1948	19.1	2	Petri dish	4	200
Brush box	*Tristania conferta* R. Br.	May 5, 1944	May 5, 1948	22.3	2	Petri dish	4	200
Turpentine tree	*Syncarpia laurifolia* Ten.	May 5, 1944	May 5, 1948	42.4	2	Petri dish	4	200
Norfolk Island pine	*Araucaria excelsa* R. Br.	Sept. 26, 1944	Nov. 26, 1945	41.0	3	Germinator	4	50
Mamani	*Sophora chrysophylla* Seem.	Dec. 12, 1944	June 12, 1948	100.0	4	Petri dish	4	25
Monterey cypress	*Cupressus macrocarpa* Hartw.	Jan. 24, 1945	June 24, 1948	6.0	4	Petri dish	4	200
Indian sandalwood	*Santalum album* Linn.	July 18, 1945	June 18, 1948	100.0	3	Petri dish	2	10

*All tests at room temperature (70°–80° F.).

tained by the use of "running averages" of the original data.

Paper bark seed

The germination behavior of this seed in storage at various temperatures and relative humidities is graphically presented in Figure 1. At each storage temperature, the relative humidity has influenced the viability of the stored seed (Fig. 1). In general, the lower the humidity, the longer the seed is kept in a germinative condition. At room temperature, the 45 per cent relative humidity gave results slightly superior to the 30 per cent relative humidity. At 59° F., these two humidities were equally effective in prolonging the life of the seed. The 45 and 60 per cent relative humidities were slightly more effective than the 30 per cent relative humidity for maintaining the viability of the seed in storage at 45° F. At each storage temperature, the seed kept in an airtight container maintained its viability just as well as that kept at 75 per cent relative humidity. The longevity curve for the seed stored open at room temperature lies approximately midway between the 60 and 75 per cent relative humidity curves. Since the relative humidity of the air is approximately 68 per cent, it seems logical to assume that the curve for the open storage should be in this position. Although no attempt was made to maintain the humidity in the cold chamber and no humidity measurements were made, it may be surmised that seed stored open at 59° F. was subjected to relative humidities in the neighborhood of 30 and 45 per cent because the curves for these storage media lie in about the same plane (Fig. 1). At 45° F., the curve for the open storage lies in the neighborhood of the lower humidity storage curves after the first year of storage.

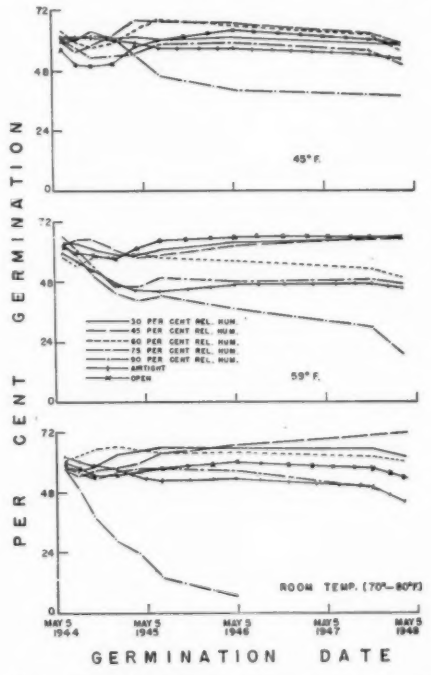

FIG. 1. The effect of temperature and relative humidity on the viability of stored paper bark seed.

When the graphs in Figure 1 are superimposed and a critical examination is made of them, it becomes evident that the effectiveness of the two lowest relative humidities (30 and 45 per cent) in preserving the viability of the seed was not influenced by the different storage temperatures. At relative humidities of 60 and 75 per cent and under airtight conditions, 45° F. and room temperature were each equally more effective than 59° F. in preserving the life of the seed. At a relative humidity of 90 per cent, 45° F. was more effective than 59° F., which in turn was more effective than room temperature in maintaining the longevity of the seed. In open storage, 59° F. maintained the viability of the seed more effectively than 45° F. and room temperature, which were equal to each other in effectiveness.

It can be seen from Figure 1 that the viability of the seed of paper bark could be maintained for about 4 years even in open storage at room temperature. The optimum storage condition at room temperature, however, was one in which the relative humidity was kept below that of the air. Generally

speaking, at temperatures of 59° and 45° F., open storage was about as effective as the low relative humidities in preserving the life of the seed.

Brush box seed

The germination behavior of the seed of brush box in storage under various conditions is depicted graphically in Figure 2. In general, regardless of the storage temperature, seeds stored at the low relative humidities maintained their viability better than those stored at the high humidities (Fig. 2). At each temperature, the 45 per cent relative humidity was optimum, being superior even to the 30 per cent. The difference between these two humidities in their effectiveness in increasing the longevity of the seed, however, became smaller as the storage temperature was lowered. At room temperature, the germination curve of the seed stored in airtight containers

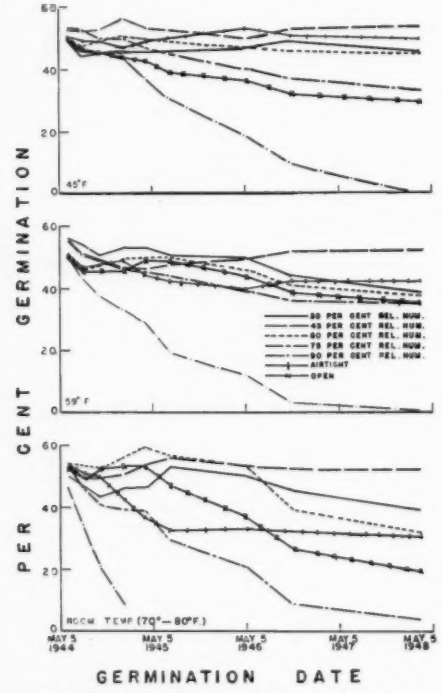

FIG. 2. The effect of temperature and relative humidity on the viability of stored brush box seed.

approached that of the seed in the 60 per cent relative humidity storage toward the latter part of the storage period. With prolonged storage at 59° F., the airtight storage curve was near the 30 per cent relative humidity storage curve. At 45° F., the airtight storage was surpassed only by the 45 per cent relative humidity storage in effectiveness in maintaining the viability of the seed. As in the case of the paper bark seed (Fig. 1), the germination curve of the seed stored open at room temperature lies approximately midway between the curves of the 60 per cent and 75 per cent relative humidity storage (Fig. 2). At 59° F., the open storage curve again lies between the 60 and 75 per cent realtive humidity curves, but at the end of the storage period, it had approached the curve of the higher one of these humidities. At 45° F., the open storage curve actually lies below that of the 75 per cent relative humidity curve.

When the graphs in Figure 2 are superimposed, it is seen that when the seeds were stored at 30 per cent relative humidity, 45° F. was more effective than 59° F. and room temperature in maintaining the viability of the seeds. The two latter temperatures were about equally effective in this respect. The effectiveness of the 45 per cent relative humidity in prolonging the germinative power of the seed was not influenced by the different temperatures employed. At relative humidities of 60 and 90 per cent and in airtight storage, it was found that the lower the storage temperature, the longer the seeds remained viable. Temperatures of 45° and 59° F. were equally more effective than room temperature; in open storage seeds kept at 59° F. remained in a viable state longer than those kept at 45° F. Seeds stored open at the latter temperature in turn kept better than those stored at room temperature.

Since the longevity of the seed at 45 per cent relative humidity was the same at any storage temperature and since this humidity was the optimum for seed storage, it followed that even at room temperature, the seed of

brush box could be kept viable for several years provided it was stored at this humidity. Another effective method of prolonging the life of the seed was to store it in airtight containers at 45° F. (Fig. 2).

Turpentine tree seed

The germination results of this seed in storage under various conditions are shown in Figure 3. Seeds stored at different relative humidities behaved differently at different temperatures. In general, at room temperature, the lower the humidity the better the seed kept, although toward the latter part of the storage period, the 45 per cent relative humidity seemed somewhat superior to the 30 per cent humidity. After a prolonged storage period at room temperature, the viability of the seeds in airtight and open storage was approximately the same, and the germination

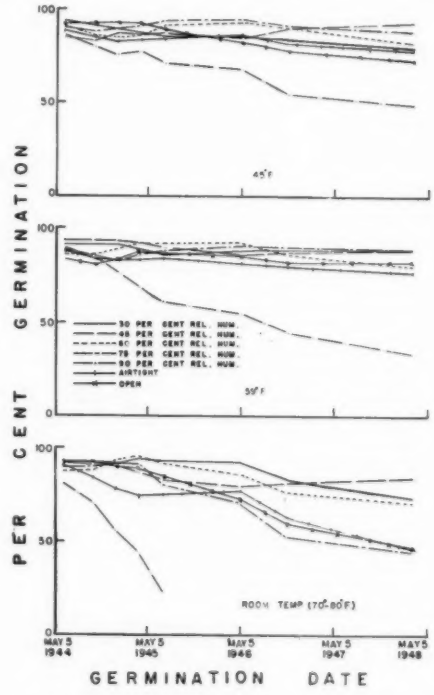

FIG. 3. The effect of temperature and relative humidity on the viability of stored turpentine tree seed.

curves for these seeds lie above the 75 per cent relative humidity curve and below the 60 per cent humidity curve (Fig. 3). Seeds stored at relative humidities of 30, 45, and 75 per cent maintained their original germination after 4 years of storage at 59° F. Storage at a relative humidity of 60 per cent and storage in airtight and open containers were slightly less effective than the above humidities at this temperature. Storage at 90 per cent relative humidity at 59° F. was detrimental to the keeping quality of the seed. With prolonged storage at 45° F., relative humidities of 45 and 75 per cent seemed to be about the optimum media for maintaining the longevity of the seed; relative humidities of 30 and 60 per cent and airtight storage seemed to be the next best storage media. Open storage at this temperature was slightly inferior to the above storage conditions. Storage at 90 per cent relative humidity was inferior to all in retaining the viability of the seed.

When the graphs in Figure 3 are superimposed, it is seen that at a relative humidity of 30 per cent, 59° F. was more effective than 45° F. or room temperature in retaining the viability of the seed. At relative humidities of 45, 60, and 75 per cent and in airtight storage, the seed kept in a viable condition longer at 45° and 59° F. than at room temperature. The two lower temperatures were equally effective in this respect. The loss of viability of the seeds stored at a relative humidity of 90 per cent was proportional to the storage temperature; that is, the higher the temperature, the more rapid was the loss in viability. With open storage, 59° F. was slightly superior to 45° F., which in turn was superior to room temperature in maintaining the life of the seed.

From the above considerations, it seemed that an optimum storage medium for the seed of turpentine tree was one in which the relative humidity was maintained at either 30, 45, or 75 per cent at 59° F., or one in which the relative humidity was maintained at either 45 or 75 per cent at 45° F.

Norfolk Island pine seed

The germination behavior of the seed of Norfolk Island pine in storage at various relative humidities and temperatures is presented in Figure 4. At room temperature, no matter what the storage condition, the longevity of the stored seed was very short (Fig. 4). At this temperature, open storage seemed to be slightly superior to the other types of storage. At 59° F., the lower relative humidities, especially the 45 per cent, preserved the viability of the seed better than the higher humidities. At 45° F., the most striking occurrence was the position of the 30 per cent relative humidity curve. As a storage medium, this humidity was inferior to all the other storage media. The 60 per cent relative humidity at 45° F. seemed about the optimum storage medium, with the 75 per cent humidity a close second. In general, up to a relative humidity of 75 per cent, the higher the humidity, the better the seed kept in a viable state. At a relative humidity of 90 per cent, the seed did not keep any better than that in open storage. Though inferior to the 60 and 75 per cent relative humidities, the airtight storage was superior to the open storage for maintaining the longevity of the seed at 45° F.

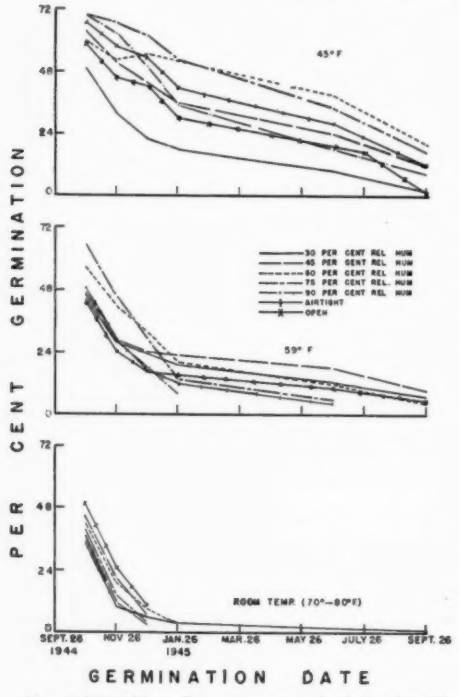

FIG. 4. The effect of temperature and relative humidity on the viability of stored Norfolk Island pine seed.

When the graphs in Figure 4 are superimposed, it will be seen that, in general, the germination curves of the seeds stored at 45° F. lie above those of the seeds stored at 59° F. and that the latter curves in turn lie above those of the seeds stored at room temperature. Thus it seems that regardless of the storage medium, the lower the temperature, the longer was the seed kept in a viable condition.

From the above considerations, it seemed that storing the seed of Norfolk Island pine at a relative humidity of 60 per cent at 45° F. extended the germinative life of this seed.

Mamani seed

In Figure 5 is presented graphically the germination behavior of the seed of mamani in storage under various conditions. Unfortunately, shortage of seed supply necessitated the termination of some germination tests before the experiment was concluded. As a result, in these instances, accurate comparisons between the different storage media could not be made. Nevertheless, it seems that in open storage this seed remained viable for an extended period of time even at room temperature. At the lower temperatures of 45° and 59° F., open storage was probably superior to the other storage media.

When all the storage media are taken into consideration, it seems that as a whole the lower temperatures of 45° and 59° F. were slightly superior to room temperature in maintaining the longevity of mamani seed (Fig. 5). These low temperatures were equally effective in prolonging the viability of this seed.

From the above considerations, it followed

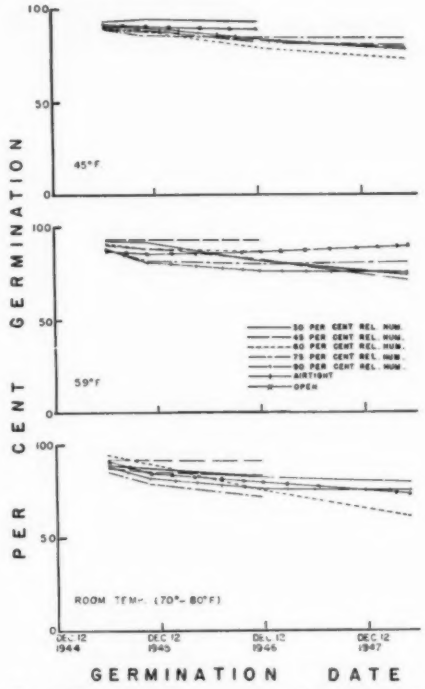

FIG. 5. The effect of temperature and relative humidity on the viability of stored mamani seed.

that storage of mamani seed in the open at temperatures of 59° or 45° F. seemed to be the optimum storage condition for maintaining the viability of this seed over an extended period of time.

Monterey cypress seed

The germination behavior of Monterey cypress seed in storage under various conditions is presented in Figure 6. At room temperature, the lowest and the highest relative humidities were the least effective in maintaining the viability of this seed. The 45 and 75 per cent relative humidities were more effective. The 60 per cent relative humidity was the most effective storage medium at room temperature. The airtight storage and open storage were inferior to only the 60 per cent relative humidity. At 59° F., the 30 per cent relative humidity was the least effective storage medium, and the 60 per cent relative humidity was the most effective. The position of the germination curves of the 45, 75, and 90 per cent relative humidities was approximately midway between the curves of these two humidities (Fig. 6). The curve of the airtight storage approached that of the 30 per cent relative humidity, and the curve of the open storage approached that of the 60 per cent relative humidity. At 45° F., the most effective medium was the open storage, and the least effective was the airtight storage. The 30, 45, and 60 per cent relative humidities were equally less effective than the open storage. The highest relative humidities, 75 and 90 per cent, were somewhat superior to the airtight storage toward the latter part of the storage period in maintaining the viability of the seed at 45° F.

When the graphs in Figure 6 are superimposed, it appears that at relative humidities of

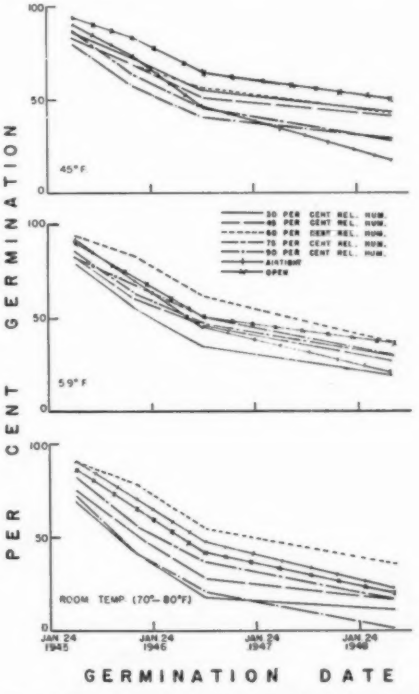

FIG. 6. The effect of temperature and relative humidity on the viability of stored Monterey cypress seed.

30 and 45 per cent and in open storage, the lower the temperature the longer the seed remains viable. At a relative humidity of 60 per cent and with airtight storage, the three storage temperatures were equally effective in preserving the viability of the seed. At 75 per cent relative humidity, temperatures of 45° and 59° F. were equally more effective than room temperature. At 90 per cent relative humidity, 59° F. was more effective than 45° F., which in turn was more effective than room temperature.

From the above considerations, it seemed that storing the seed of Monterey cypress in the open at 45° F. prolonged the life span of this seed better than storing under any other condition.

Indian sandalwood seed

Because of the limited supply of Indian sandalwood seed, only a few seeds were used in the germination tests (Table 1). Nevertheless, the results obtained seemed reliable.

The germination status of this seed at various periods of storage under varying conditions is depicted graphically in Figure 7, which indicates that at room temperature, the low relative humidities of 30, 45, and 60 per cent seemed to be the optimum storage media. The high relative humidities of 75 and 90 per cent were the least effective in preserving the life of the seed. The airtight storage and open storage were intermediate between these humidity groups in this respect. At 59° F., the lower the relative humidity the longer the seed kept viable. The airtight storage and open storage were less effective than the 45 per cent relative humidity but more effective than the 60 per cent humidity at this temperature. In general, the lower relative humidities were more effective than the higher humidities in maintaining the viability of the seed at 45° F. The optimum relative humidity was probably 45 per cent. Seeds stored in airtight containers and in the open retained their viability approximately to the same degree as those stored at the relative humidity of 60 per cent at this temperature.

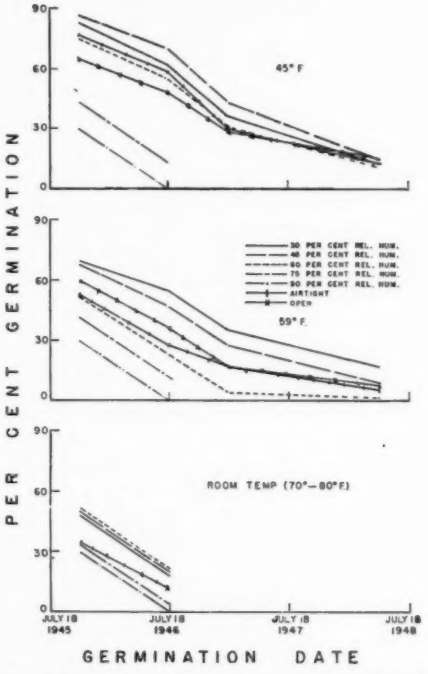

FIG. 7. The effect of temperature and relative humidity on the viability of stored Indian sandalwood seed.

When the germination curves of the seeds stored at the same humidities at each temperature are compared with each other, it will be seen that at relative humidities of 30, 45, and 60 per cent, 45° F. was more effective than 59° F., which in turn was more effective than room temperature in maintaining the viability of the seed (Fig. 7). At a relative humidity of 75 per cent, 45° and 59° F. were equally more effective than room temperature. At a relative humidity of 90 per cent, the three temperatures were equal in effectiveness. In airtight storage and in open storage, the lower the temperature the longer the seed remained viable.

From the above considerations, it can be stated that the optimum storage condition for Indian sandalwood seed was one in which the

temperature and the relative humidity were maintained at 45° F. and 45 per cent, respectively.

DISCUSSION

If the longevity of the seeds of all species under all conditions of storage is considered as a whole, it will be seen that these seeds fall in one of the following groups: long-lived seed, medium-lived seed, and short-lived seed. The seed of mamani falls in the first group. In the second category fall the seeds of paper bark, turpentine tree, and brush box. The seeds of Monterey cypress, Indian sandalwood, and Norfolk Island pine are short-lived.

The retention of viability by the seed of mamani was probably due to the impervious nature of its seedcoat, which interfered with the uptake of moisture and with respiration. It will be remembered that this seed required scarification for germination. Generally speaking, regardless of the condition of storage, this seed maintained its viability for 3½ years (Fig. 5).

In general, among the medium-lived seeds, the seeds of paper bark and turpentine tree maintained their viability in storage for 4 years, slightly better than the seed of brush box (Figs. 1, 2, and 3).

In general, among the short-lived seeds, the seed of Monterey cypress retained its viability better than that of Indian sandalwood, which in turn maintained its viability better than the seed of Norfolk Island pine (Figs. 4, 6, and 7).

Although different species reacted somewhat differently toward the various storage conditions, in general, the lower relative humidities were more conducive than the higher humidities to the preservation of viability. There were, however, two species (Monterey cypress and Norfolk Island pine) which were exceptions to this statement. Monterey cypress seed stored at 30 per cent relative humidity at room temperature did not maintain its viability any better than that stored at 90 per cent relative humidity at this temperature (Fig. 6). The 30 per cent relative humidity at 59° F. was the least effective storage medium for this seed. At a temperature of 45° F., the 30 per cent relative humidity was also the least effective storage medium for the seed of Norfolk Island pine (Fig. 4).

SUMMARY

The effects of temperature and relative humidity on longevity of seeds of seven forest tree species in storage for several years were studied.

Although seeds of different species reacted somewhat differently toward the various storage conditions, in general it can be stated that the longevity of these seeds can be maintained in Hawaii if the temperature of the storage medium is maintained at a lower level than that of the prevailing atmosphere (70°–80° F.), if the relative humidity is maintained at a lower level than that of the prevailing atmosphere (66–71 per cent), or if both the temperature and relative humidity are maintained at lower levels than those of the air.

The following were found to be the optimum media for the storage of seeds of the individual species in Hawaii:

Paper bark—Relative humidity of 45 per cent at room temperature or open storage at 59° F.

Brush box—Relative humidity of 45 per cent at room temperature or airtight storage at 45° F.

Turpentine tree—Relative humidity of 45 per cent at 59° F.

Norfolk Island pine—Relative humidity of 60 per cent at 45° F.

Mamani—Open storage at 59° F.

Monterey cypress—Open storage at 45° F.

Indian sandalwood—Relative humidity of 45 per cent at 45° F.

REFERENCES

AKAMINE, E. K. 1942. *Methods of increasing the germination of koa haole seed.* Hawaii Agr. Expt. Sta. Cir. 21: 1–14.

——— 1943. *The effect of temperature and humidity on viability of stored seeds in Hawaii.* Hawaii Agr. Expt. Sta. Bul. 90: 1–23.

BALDWIN, H. I. 1942. *Forest tree seed.* xvi+240 pp., 28 figs. Chronica Botanica Co., Waltham, Mass.

CROCKER, W. 1948. *Growth of plants.* v+459 pp., 171 figs. Reinhold Publishing Corp., New York.

HEIT, C. E., and E. J. ELIASON. 1940. Coniferous tree seed testing and factors affecting germination and seed quality. *N. Y. State Agr. Expt. Sta. Tech. Bul.* 255: 1–45.

ISAAC, L. A. 1934. Cold storage prolongs the life of Noble fir seed and apparently increases germinative power. *Ecology* 15: 216–217.

LATOUR, H. J. 1942. Notes on the storage of red pine seed for 9 years. *N. Y. State Conservation Department Notes on Forest Investigations* 38: 1. [Mimeographed.]

MOSS, E. H. 1938. Longevity of seed and establishment of seedlings in species of *Populus. Bot. Gaz.* 99: 529–542.

PORTER, R. H. 1949. Recent developments in seed technology. *Bot. Rev.* 15: 221–344.

TOUMEY, J. W., and C. F. KORSTIAN. 1931. *Seeding and planting in the practice of forestry.* 2d ed. xviii+507 pp., 162 figs. John Wiley and Sons, New York.

Pacific Symphytognathid Spiders

B. J. MARPLES[1]

THE FAMILY SYMPHYTOGNATHIDAE was erected by Hickman (1931) for a minute spider, *Symphytognatha globosa*, from Tasmania. The most characteristic feature is the absence of lung-books, the anterior spiracles leading into tracheal tubes which supply the cephalothorax as well as the abdomen, while the posterior spiracles are absent. In *S. globosa* the female has no palps. Fage (1937) and Gertsch (1941) have transferred several other genera into this family, or described new ones. In some of these only four eyes are present instead of the usual six, and the female palps may be merely reduced in size instead of absent.

Some of the specimens described in the present paper were collected in 1946 in Upolu, Western Samoa, during a visit devoted to the collection of arachnids; a few hours of collecting in Suva, Fiji, on the return journey, yielded specimens of a closely related but quite distinct species. Because this is a peculiar and interesting family which has not previously been recorded from the Pacific islands, it seemed desirable to deal with both species together. The main Samoan collection is being dealt with as a whole.

In the following descriptions the leg index, given below the leg formula, is the length of the leg divided by the length of the carapace. The tibial index is the breadth of the proximal end of the patella expressed as a percentage of the combined lengths of the tibia and patella.

Patu gen. nov.

Six eyes. Chelicerae fused for about half of their length. Ventral end of the retromargin of the cheliceral groove with a large bifurcated process. Palp of female absent. Three claws, ventral one large. Abdomen pear-shaped with ventral spinnerets. Close to genus *Symphytognatha*, but different in web and coccoon and in a number of minor structural characters. Genotype: *Patu vitiensis*.

Patu vitiensis n. sp.

Three ♀, 1♂, 1 immature♂. From tree trunks, Suva, Fiji.

FEMALE: Length 1.20 mm. Carapace, sternum, and mouth parts brown, legs lighter. Abdomen mottled greyish-brown above, darkening towards the posterior end. Ventral surface behind the spinnerets very much lighter, almost cream-coloured.

Carapace: Length 0.37 mm., breadth 0.32 mm. Highest near the eyes, which are near the anterior margin.

Eyes: Six, all pale. Posterior row recurved. Lateral eyes touching. PME separated from one another by one quarter of their diameter and from the PLE by rather more than their diameter. Ratio of eyes PLE:ALE:PME = 71:68:60. Eye group breadth 0.23 mm.

Chelicerae: No boss or stridulating organ. Apparently fused for rather less than half of their length. Fang stout with relatively large serrations, and longer than the groove. The ventral retromargin of the groove with a stout process bifurcated into two blunt teeth.

Maxillae: Converging but not meeting above the lip.

Lip: Broader than long.

Sternum: Length 0.23 mm., breadth 0.22 mm. Convex.

Palp: No vestige visible even in cleared

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specimens, though a stout hair arises in the same spot.

Legs:	1	4	2	3
	2.9	2.8	2.6	2.1

seen in a cleared specimen as in the figure. Pair of striated structures on the pedicel as in *S. globosa*, where they were interpreted by Hickman (1931) as lyriform organs and by Petrunkevitch (1933) as stridulating organs.

	FEMUR	PATELLA AND TIBIA	METATARSUS	TARSUS	TOTAL
I	0.35	0.37	0.21	0.19	1.12
II	0.31	0.35	0.14	0.19	0.99
III	0.28	0.24	0.08	0.17	0.77
IV	0.35	0.35	0.14	0.21	1.05

Tibial Index I.....13.1 Tibial Index IV.....13.6

Three claws, the median one being long, sharp and downcurved, and larger than the paired ones. The median claw on legs I and II has one tooth; all the other claws are without pectinations. A few serrated bristles on the feet. No spines, but a large erect bristle towards the distal end of each patella, two smaller ones on tibia I, and one on tibia II. One trichobothrium on metatarsi I and II, three on tibiae I and II, two on III, and four on tibia IV.

Abdomen: Length 0.88 mm., breadth 0.56 mm. Pear-shaped with a rounded posterior end. The six spinnerets are ventrally placed, the anterior being the largest. Anal tubercle widened transversely. No colulus. Epigyne in the form of a transverse furrow overhung from in front by a rounded lip. Internal structure

MALE: Length 0.76 mm. Carapace, sternum, and mouth parts brown, legs light brown. Abdomen light yellowish-brown, posterior end black. Anterior part of the sides slightly darker, there being a very faint suggestion of a dorsal band joining these areas. More well marked are two triangular dark areas anterior to the posterior black cap. Together they form a procurved crescentic dark marking, interrupted in the mid-dorsal line by the yellowish-brown ground colour of the abdomen.

Carapace: Length 0.30 mm., breadth 0.31 mm. Sloping up steeply to the conspicuous row of eyes. Anterior to the eyes is a sinuous ridge, concave above the chelicerae and curving forward in the middle line. This has the appearance of being the anterior edge of the

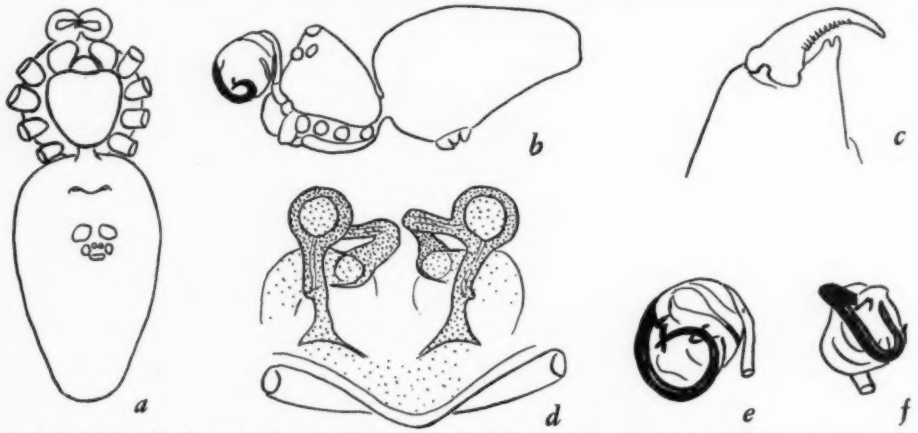

FIG. 1. *Patu vitiensis: a*, female, ventral view; *b*, male, left side; *c*, female chelicera, dorso-retrolateral view; *d*, female apparatus as seen in a cleared skin; *e*, male palp, retrolateral view; *f*, male palp, ventral view.

carapace, but below it is a more or less vertical clypeus. The details are very difficult to make out, owing to the small size.

Eyes: Six, all pale. Posterior row slightly recurved. The PME are separated from one another by about half their diameter and from the PLE by almost their diameter. The lateral eyes are touching. Ratio of eyes, PLE:PME:ALE = 75:70:51. Breadth of eye group 0.23 mm. The PME are separated from the anterior ridge by about half their diameter and from the anterior edge of the carapace by about two and a half times their diameter.

Chelicerae: Small.

Maxillae and Lip: As in female.

Sternum: length 0.24 mm., breadth 0.19 mm.

Palp: Large and rounded palpal organ, details as in figure.

Legs: 1 2 4 3
3.8 3.3 2.7 2.4

	FEMUR	PATELLA AND TIBIA	METATARSUS	TARSUS	TOTAL
I	0.31	0.36	0.16	0.23	1.06
II	0.26	0.33	0.14	0.19	0.92
III	0.20	0.23	0.10	0.15	0.68
IV	0.27	0.30	0.11	0.16	0.84

Tibial Index I.....11.3 Tibial Index IV.....12.5

One stout spine on the ventral surface of tibia II about one third of its length from the distal end.

Abdomen: Length 0.55 mm., breadth 0.33 mm. Pear-shaped with the narrower posterior end truncated. Spinnerets ventral and close to the petiolus.

Web and Coccoons: The webs were situated on tree trunks and consisted of fine horizontal sheets about 4 centimeters long. The silk was too fine for the arrangement of threads to be made out. No oblique thread was noticed as in the Samoan species, though a bunch of coccoons was hanging some way from the edge. Spiders were seen sitting in the centre instead of with the coccoons; possibly these may have been males while the females were with the coccoons.

Patu samoensis n. sp.

Eight ♀ from minute sheet webs in the irregularities of tree trunks in forest, Apia, Upolu, Western Samoa.

FEMALE: Length 1.63 mm. Carapace, sternum, and mouth parts dark brown. Legs lighter with dark annulations. Abdomen mottled greyish.

Carapace: Length 0.55 mm., breadth 0.43 mm. High and rounded.

Eyes: Six, all pale. Large and conspicuous, posterior row straight. PME separated from one another by less than a quarter of their diameter and from the PLE by less than half their diameter. Lateral eyes touching. Ratio of eyes, PME:PLE:ALE = 78:68:64. Eye groups breadth 0.30 mm. PME twice their diameter from the carapace edge.

Chelicerae: Apparently fused for about half their length and rather cylindrical in anterior view. The fang is longer than the groove and has relatively large serrations. On the ventral retromargin of the groove is a stout process bifurcated into two sharp teeth. The chelicerae do not bulge forward in front of the edge of the carapace when seen in dorsal view.

Maxillae: Converging but not meeting above the lip.

Lip: Broader than long. Junction with sternum distinct.

Sternum: Length 0.30 mm., breadth 0.29 mm. Convex.

Palp: No trace of a palp is to be seen even in a cleared specimen, though three or four hairs arise from the same spot. No palp was visible in the cleared skin of a first instar taken from a coccoon.

Legs: 1 2 4 3
2.6 2.4 2.4 1.9

	FEMUR	PATELLA AND TIBIA	METATARSUS	TARSUS	TOTAL
I	0.43	0.46	0.26	0.30	1.45
II	0.38	0.43	0.22	0.30	1.33
III	0.31	0.31	0.16	0.22	1.00
IV	0.42	0.42	0.24	0.25	1.33

Tibial Index I.....15.8 Tibial Index IV.....14.3

Three claws, the third as large as the dorsal pair and sharply directed downwards. Claws slender and not pectinated, and pectinated bristles not present. No spines, but a large erect bristle at the distal end of each patella, two smaller ones on tibia I and one on tibia II. One trichobothrium on metatarsi I and II, three on tibiae I and II, two on tibia III, and four on tibia IV.

Abdomen: Length 1.16 mm., breadth 0.80 mm. Pear-shaped, projecting behind in a knob-ended process and provided with a pair of similar dorso-lateral processes. The six spinnerets are ventral, the anterior being the largest. No colulus. Anal tubercle large. The epigyne is visible only when the abdomen is removed. There is a transverse fold overhung by a backwardly directed lip whose edge is dark and thickened. The appearance of a cleared specimen is shown in the figure.

In specimens cleared in potash the spiracles could be seen leading into an atrium from which numerous tracheal tubes supplied both the cephalothorax and abdomen. There was a transverse connecting tube between the atria. Sections showed five pairs of tracheal tubes, three large and two small, passing through the pedicel into the cephalothorax.

Web and Coccoon: The webs were spun in the irregularities of a fallen tree trunk. They consisted of a very fine horizontal sheet with very regular meshes. The sheet was an irregular polygon some 6 centimeters long, and an oblique thread extended upwards from the sheet between 1 and 2 centimeters from one end. The threads of the sheet radiated from

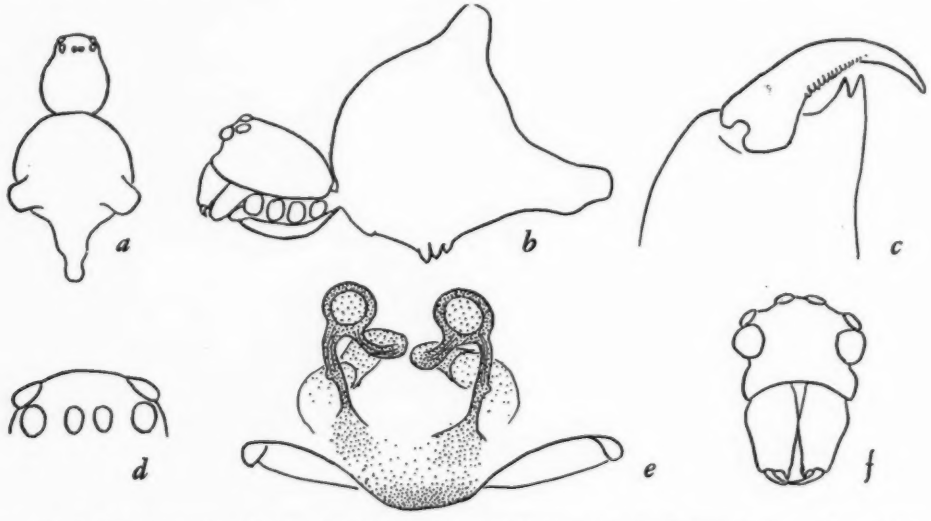

FIG. 2. *Patu samoensis: a*, female, dorsal view; *b*, female, left side; *c*, female chelicera, dorso-retrolateral view; *d*, female, eyes, dorsal view; *e*, female apparatus as seen in a cleared skin; *f*, female, anterior view of carapace and chelicerae.

the point of attachment of the oblique thread, but it was a sheet and not an orb web. The spider rested at this point together with a cluster of coccoons. The coccoons each contained only a single egg about 0.34 mm. in diameter. The coccoon consisted of a sphere some 0.66 mm. in diameter, woven loosely of fine threads so as to be transparent, the whole surface being covered with spirals of thick thread with the loops projecting from the surface. The whole structure was thus 0.83 mm. in diameter. All the silk was white. This is quite unlike the web and coccoon described by Hickman for *S. globosa*. A first instar removed from a coccoon had a globular abdomen with no trace of the projections.

SUMMARY

A new genus of spiders belonging to the family Symphytognathidae is described, with a species from Fiji and another from Samoa. Members of this family have been described from Tasmania, New Caledonia, East Indies, and Central and South America, but apparently not from the Pacific islands. The new genus seems to be close to *Symphytognatha* from Tasmania.

REFERENCES

FAGE, L. 1937. A propos de quelques nouvelles araignées apneumones. *Soc. Zool. France, Bul.* 62: 93–106.

GERTSCH, W. J. 1941. Report on some arachnids from Barro Colorado Island, Canal Zone. *Amer. Mus. Nat. Hist. Novitates* 1146: 1–8.

HICKMAN, V. V. 1931. A new family of spiders. *Zool. Soc. London, Proc.* 1321–1328.

PETRUNKEVITCH, A. 1933. An inquiry into the natural classification of spiders, based on a study of their internal anatomy. *Conn. Acad. Arts and Sci., Trans.* 31: 299–389.

The Polynesian Species of *Myoporum*[1]

GRADY L. WEBSTER[2]

INTRODUCTION

THIS REVISION was originally begun as an analysis of the notoriously polymorphic species *Myoporum sandwicense* of the Hawaiian Islands. After a considerable amount of work had been done, however, it was found that the forms of *Myoporum* from southern Polynesia were very similar. Because of the closeness of relationship, it seemed both more practical and more worth while to treat all of the Polynesian species together.

In the Hawaiian Islands, *Myoporum sandwicense* is an evergreen shrub or tree which grows mostly in dry forests on leeward slopes from sea level to an altitude of 10,000 feet. Its plasticity in habit is remarkable, as it may become a tree 15 meters high in the dry forests (Rock, 1913: 427) or a creeping, fleshy, prostrate shrub on the beaches and low rocky islets. More rarely it may even invade the rain-forest, as in Waikolu Valley on Molokai.

The Hawaiians used the species, which they called *naio*, for timber in building houses (Brigham, 1908: 83). Apparently it was not cultivated, as it is in Rarotonga (Wilder, 1931: 100), for the perfume of the flowers. There are references (Bennett, 1832: 257; Hooker and Arnott, 1841: 93) concerning the attempts of traders of the 1820's to substitute *naio* wood for sandalwood in the Chinese trade, but neither then nor since has the *naio* attained any real commercial value. Brown (1935: 279) reports that on the island of Rapa (in southern Polynesia) *naio* wood is used for building canoes and houses.

The real value of *Myoporum* to the Hawaiian Islands resides in its role in the formation of a dry forest cover and in the consequent checking of soil erosion. On most of the islands the dry forest region has been partially or completely denuded, with serious consequent erosion. Reforestation work has been carried out chiefly with quick-growing exotic trees such as *Casuarina* and *Eucalyptus*, but the appearance of the resulting vegetation is disappointing from an esthetic point of view. It is to be hoped that eventually the original dry forest trees, such as native species of *Diospyros*, *Acacia*, *Sophora*, and *Myoporum*, will regain a part of their lost dominance. Egler (1947: 425), studying the communities of the dry southeastern section of the Koolau Range on Oahu, predicted that although *Myoporum* was rare at that time it might in the future assume an important place in the *Prosopis* community.

Acknowledgments: Dr. Harold St. John of the University of Hawaii originally suggested this study, made it possible to collect and observe the plants in the field, and has been of great assistance in criticizing and offering suggestions for the manuscript. Mr. Otto Degener loaned his large and important collections for study and discussed with me some of the forms which I was unable to see in the field. Dr. B. C. Tharp readily consented to having the study continue at the University of Texas, and he and Dr. W. Gordon Whaley kindly

[1]Part of a thesis submitted in partial fulfilment of requirements for the degree of Master of Arts in Botany at the University of Texas. Manuscript received September 22, 1949.

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read and criticized the manuscript. I also wish to thank Miss Marie Neal for making available the facilities of the Bishop Museum Herbarium, Miss Mary Lou Jeffrey and Mr. William L. Brudon for drawing the illustrations, and the curators of the herbaria listed below for the loan of specimens:

Bishop Museum, Honolulu (BISH); Boisser Herbarium, Geneva (G-BOIS); Otto Degener, personal herbarium (DEG); Delessert Herbarium, Geneva (G-DEL); Gray Herbarium (GH); Royal Botanic Gardens, Kew (K); New York Botanical Garden (NY); Laboratoire de Phanerogamie, Paris (P); Riksmuseum, Stockholm (S); University of Texas, Austin (T); Naturhistorisches Museum, Vienna (W).

TAXONOMIC POSITION

The genus *Myoporum* consists of about 30 species scattered over a wide area including Mauritius, Australia, New Zealand, New Guinea, China, Japan, Micronesia, and Polynesia. It is characterized by its relatively actinomorphic corolla and its fleshy drupe with usually solitary ovules in the cells. Like other genera in the Myoporaceae, *Myoporum* has axillary flowers, stamens with confluent anther cells, pendent anatropous ovules, and gland-dotted, alternate leaves. The Verbenaceae is probably the most closely related family, but it is well distinguished by its ovules which are not apically attached and by its opposite leaves which lack internal secretory tissue (Solereder, 1899: 711).

The Polynesian species of *Myoporum* belong to section *Pentacoelium* of Gray (1866: 51), which has priority over the more appropriate name *Eumyoporum* of Bentham (1870: 2). Wettstein (1895: 360) distinguished three sections which contained Pacific insular species—*Pentacoelium*, *Polycoelium*, and *Eumyoporum*—but there is no justification for placing these insular species in more than one section. Kraenzlin's sections (1929: 15) are even more poorly founded, so it seems that so far no really satisfactory subdivision of the genus has been made.

The Hawaiian species *M. sandwicense* was apparently first collected by Archibald Menzies on Vancouver's expedition and was at first referred to the New Caledonian *M. tenuifolium* by Hooker and Arnott (1841: 93). It was described as a new species, *Polycoelium sandwicense*, by De Candolle (1847: 705) and was redescribed in the genus *Myoporum* by Asa Gray (1866: 52). No other name was officially proposed for any of the Hawaiian plants until Lévéille (1912: 63) published *M. Fauriei* based on a Faurie specimen from the island of Hawaii. Kraenzlin (1929: 21)reduced the species to a variety but appears to have misapplied the name to specimens of var. *sandwicense*.

Hugh Cuming had collected *Myoporum* in the Austral Islands (Tubuai) in 1828, but over a hundred years went by before any new species were described from southern Polynesia. Cheeseman (1903: 291) listed as *Myoporum* sp. a Mangaian plant cultivated on Rarotonga. Wilder (1931: 100) referred the Rarotongan plant to *M. sandwicense*, but Skottsberg (1933: 165) described it as a new species—*M. Wilderi*—and discussed its probable relationships to most of the other insular species. Two years later Brown (1935: 277) published three species from the Austral Islands and Rapa.

Variation in the Hawaiian myoporums has been discussed by Skottsberg in his paper on *M. Wilderi* and by Degener (1930: 261), but neither has published any new names although Degener illustrated a pubescent-leaved form and announced his intention of describing it in his *Flora Hawaiiensis*.

MORPHOLOGICAL CRITERIA

Because of the extreme polymorphism of many Hawaiian populations of *Myoporum* it is difficult to find morphological characters which do not vary as much between individuals as between varieties. An accurate concept of the range of variation—arrived at

by observation of a great many specimens—is essential in defining the taxonomic characters of the various groups.

Growth habit, as has been indicated, is so greatly modified by environment that it is probably of no taxonomic significance. The stem is significant only in distinguishing var. *stellatum* from var. *Degeneri*, the former having pubescent branchlets.

There are many leaf shapes but few of them are constant in any one population. Serrate margins are found sporadically among nearly all the Hawaiian varieties and must be used with extreme caution as a taxonomic character. On the other hand, this serrature is constant in the southern Polynesian forms and may be used dependably to separate *M. Stokesii* from *M. rapense*. Conspicuous differences in leaf texture occur among the Hawaiian plants, but in the main these appear to reflect environmental differences. The relative conspicuousness of the nervation depends in turn on leaf texture and is thus obviously unreliable.

The leaves of all the Polynesian species have subepidermal pellucid-punctate tissue, and the distribution and type of these pellucid spots appear to be good specific criteria. *M. Stokesii* and *M. rapense* are difficult to separate from the New Zealand *M. laetum* except for the fact that the glandular spots on the leaves of the latter are far more conspicuous. In *M. laetum* the pellucid spots are visible by reflected light (on the upper leaf surface) and give a distinct "polka dot" effect in transmitted light. The spots of the two Polynesian species are smaller, less conspicuous in transmitted light, and almost invisible in reflected light.

A readily recognizable and often valuable leaf character in Hawaiian *Myoporum* is the presence of pubescence. Unfortunately, while pubescent leaves are constant features of varieties *stellatum* and *Degeneri* they may appear sporadically in populations of other varieties which ordinarily have glabrous leaves. These sporadic occurrences seem often to be a response to wounding caused by grazing animals, although in some cases the lower "sucker" shoots from an uninjured plant may bear pubescent leaves. In fact, even if the leaves on basal or wound shoots are not pubescent, they are often serrate and larger than normal leaves. Furthermore, there is evidence that at least in some groups of *Myoporum sandwicense* the "juvenile" leaves of a young plant are of the abnormal serrate-pubescent type, while those formed later are entire and glabrous. Further investigations on this subject are much to be desired.

The number of flowers in the axillary clusters varies not only between plants but even on the same branch and thus does not appear to be of any great taxonomic value. The same can be said of the flower pedicels, which vary widely, but inconsistently, in length and thickness.

The number and length of the calyx lobes, within certain ranges of variation, are significant, while their shape (on account of its plasticity) is usually less so. The size and shape of the corolla have not been used for distinguishing varieties; although there are readily apparent differences, they are overlapping and inconstant. The amount of pubescence on the corolla throat is usually quite variable and may or may not have significance.

The ovary is generally uniform in shape and constant in size, within any one variety. It is glabrous and has a somewhat expanded, differently colored basal region which seems to be nectariferous. At anthesis the flowers may be noticeably fragrant, although I have personally found the flowers of *M. sandwicense* to be almost odorless. In marked contrast to the Hawaiian species in this regard are *M. Stokesii* and *M. rapense*, whose flowers are credited in collectors' notes as ranging in scent from "strong sweet" to "fetid."

The style furnishes some of the best taxonomic criteria, especially in its length and in the presence or absence of pubescence.

This last character is undoubtedly valuable in delimiting species, although it may occasionally be inconstant (on the islands of Hawaii and Raivavae). The abrupt basal curvature of the style observed in some of the specimens from southern Polynesia is an inconstant character and its importance is hard to assess on the basis of the small amount of material studied.

The number of stamens is one of the classical key characters for separating *M. sandwicense* from the other Polynesian species, but this distinction breaks down when a large number of Hawaiian specimens is examined. The length and height of insertion of the stamens were found to be quite inconstant, and the degree of divergence of the anther cells is dependent on age and is of no taxonomic value at all.

The drupes of most of the Hawaiian varieties differ from the other Polynesian species in having a greenish-white exocarp. Some plants on the island of Hawaii (var. *Fauriei*), however, may have either whitish, pink, or purplish drupes. The drupes of *M. Stokesii* and *M. rapense* are pink or red and brick-red or purplish-red, respectively, while those of *M. laetum* are said to be purple. Judging from the variability of color in *M. sandwicense* var. *Fauriei*, however, it would be unwise to consider differences in shade of color as especially meaningful. The presence of color in the drupes of var. *Fauriei* and its absence in the other Hawaiian varieties do seem to be significant, however.

The bony endocarp is usually subglobose or top-shaped and often ridged at the top or along the sides. Its shape, although extremely variable, is a distinguishing character in some varieties and species. The number of cells in the drupe is inconstant, but a knowledge of the range of variation will assist in placing a specimen in the proper category. Counting the number of cells is not always easy as some of the abortive ones may be quite small. There is often a considerable degree of sterility, for many drupes will be found to contain only one or two cells with well-developed seeds.

TAXONOMIC CATEGORIES

The *species* is here considered to be a population whose individuals have in common an ensemble of fundamental morphological characters different from that present in other species. It is reasonable to suppose that this morphological distinctiveness is due to various types of barriers (such as geographical, physiological, and genetical) which prevent a free genetic exchange with other species.

The categories *subspecies* and *variety*, as here used, apply to groups which occupy a discrete region within the total area of the species and which are characterized by a lack of sharp morphological distinctness from other groups within the species. A subspecies differs from a variety in its greater morphological differentiation, but does not necessarily occupy a greater area. Both are considered to lack genetic isolation—that is, varieties of the same species would be expected to interbreed freely when brought together—and no doubt often owe their existence to geographical barriers.

In recent years there has been considerable discussion among taxonomists as to whether the geographically delimited groups within a species should be given the rank of subspecies or of variety. However, in this work it has seemed better to use both categories in order better to accommodate the great sub-specific range of differentiation.

The *form*, in the present intrepretation, is a group of plants which occur within a variety and differ by very minor or inconstant characters; they may or may not be geographically localized. Specimens may also be referred to forms when they are inadequate to give an accurate concept of the population. Inasmuch as the forms listed in this study are not conveniently separated morphologically and to some extent are designations based on incomplete knowledge, it seems unwise to

dignify them with Latin names. For convenience they are listed by number, each under the island where it occurs.

DISTRIBUTION

So far species of *Myoporum* have not been discovered on any of the islands occurring in the 3,000-mile expanse of sea between Hawaii and the Austral Islands. It is not surprising that they are missing from low coral atolls such as Palmyra and Fanning, but their absence from the Society Islands, the Marquesas, and Makatea is unexpected, as is their absence from other large Pacific islands such as Samoa and Fiji.

The disjunct distribution of *M. sandwicense*—with two subspecies in the Hawaiian Islands and one in the Cook Islands (Mangaia)—is not unique, however. For instance, *Isachne distichophylla* has been found only on Rarotonga and in the Hawaiian Islands. *Hedyotis* section *Bikkiocarpa* has two species, one from West Maui and one from Rapa (see Fosberg, 1943: 25). The genus *Phyllostegia* has 23 species in the Hawaiian Islands and one in Tahiti. Our present state of knowledge is insufficient to explain these facts of distribution. However, the theory of Zimmerman (1948: 49–52) that high volcanic islands, now reduced to reefs or atolls by erosion, once existed as stepping-stones in the mid-Pacific indicates how these cases of bicentric distribution might have arisen.

At the time of Captain Cook's visit *Myoporum* undoubtedly existed on all seven of the main Hawaiian Islands. It is now absent from the denuded island of Kahoolawe, but Forbes (1913: 86) learned from old visitors to the island that the *naio* had been seen there before the dry forest was wiped out. The relative abundance of the species at those localities where it still persists has no doubt undergone great changes. In some areas, as at Kaena Point on Oahu and the Puuwaawaa district of Hawaii, it may be as common as it was before the dry forests were disturbed; on the other hand it is rare or absent from areas such as the Lualualei region on Oahu, western Molokai, and the Kohala peninsula of Hawaii, where probably it was once very abundant.

In the Austral Islands the destruction of the native forests has been so complete that a clear picture of the distribution of *Myoporum* there may never be obtained. St. John tells me that he made a special effort to collect *Myoporum* on these islands during the Mangarevan Expedition of 1934 and that few plants of the genus could have been overlooked in the vestiges of the native forest. Judging from his findings, *M. rapense* var. *Skottsbergii* and the form described by Brown as *M. rimatarense* may well be extinct.

On the basis of our present knowledge, however, it seems significant that *M. rapense* is found on the three lower islands of the Austral group and that its derivative *M. Stokesii* is restricted to Raivavae.

One of the chief difficulties in understanding the distributional pattern of Polynesian *Myoporum* is that the means of long-range dispersal of the genus are still a matter of conjecture. It does not appear likely that the fruits are spread by ocean currents, since my own observations show that they will float for no more than a few days. Dispersal by birds is a possibility, since some endemic Hawaiian birds were known to have eaten the seeds; but there is no evidence that any migratory birds are fond of the fruits. It must be admitted that the dispersal mechanism of *Myoporum* still remains unknown, and that the accidental transport by hurricanes is as likely a possibility as any.

RELATIONSHIPS OF THE SPECIES

At present, and in spite of a fairly recent monograph (Kraenzlin, 1929), the genus *Myoporum* is in great need of critical revision. The seat of the greatest systematic difficulty is the complex of chiefly insular species which includes the three Polynesian species. Almost nowhere within this insular complex are the species well defined, and it is very difficult to

find morphological characters sufficiently constant to distinguish them.

Because of its great range of morphological variation, *M. sandwicense* poses a particularly difficult problem in species definition. In its most typical form the species is well characterized by its flowers with five stamens and a glabrous style, and by its whitish-colored drupes with five or more cells. To some extent, however, every one of these characters proves to be inconstant when the complete range of variation of the species is ascertained. The other Polynesian species typically differ in having flowers with four stamens and pubescent styles as well as reddish-tinted drupes with fewer cells, but most of these characters are inconstant. However, *M. sandwicense* not only approaches the other Polynesian species very closely, but also is hard to separate from *M. tenuifolium*, a species lying to the west and southwest in Micronesia and Melanesia. This latter species is characterized by the small size of its flowers and fruits; but there are forms of *M. sandwicense* whose reproductive organs are of about the same dimensions. Of course, in all these cases species distinctions can be maintained by using rather complicated combinations of characters; for instance, *M. tenuifolium* can be separated from *M. sandwicense* by the fact that the forms of the latter which have small flowers and fruit do not have pink-tinted drupes. Such contrived species differences are admittedly unsatisfactory, but they will have to serve for the present. The temptation to combine various of the insular species should be resisted until the entire group is surveyed, because only then will it be possible to define the exact limits of *M. sandwicense* and its nearest congeners.

Because the classification of the insular myoporums is still in a very imperfect state, one hesitates to speculate as to the phylogeny of the Polynesian groups. However, the following observations on the possible relationships of the Hawaiian groups seem worthy of statement.

It is pretty clear that the group of *M. sandwicense* showing the greatest resemblance to the Austral Island species is ssp. *Wilderi*, although it is not possible to say whether or not the latter originated directly from or coordinately with the Austral Island species. Among the groups of *M. sandwicense* from the Hawaiian Islands proper, var. *Fauriei* shows the greatest resemblance to ssp. *Wilderi*. Because var. *Fauriei* is restricted to the island of Hawaii, it seems likely that this island was the point of immigration of *Myoporum*. Degener (1930: 266), on the basis of the occurrence of pubescent, serrate leaves on certain wounded plants from Molokai, has suggested that the direct ancestor of the Hawaiian forms had leaves of this type. However, this phenomenon does not seem to be a case of a reversion to an immediate ancestral type, but rather the expression of a potentiality which is widespread, inasmuch as independent occurrences of pubescent leaves are known from other Hawaiian islands as well as from Australia, New Zealand, and New Caledonia.

It seems evident that var. *sandwicense*, the most widely distributed of the Hawaiian groups, is derived from var. *Fauriei*, while it in turn has given rise to varieties *lanaiense*, *Degeneri*, and *stellatum*. The origin of ssp. *St.-Johnii* is more obscure. It could have come directly from the adjacent population of var. *Fauriei*, but the rather great morphological differences between the two entities make this rather questionable. The history of *Myoporum* on the island of Hawaii is made even more mysterious by the fact that var. *sandwicense* is absent from this island, even though it is presumed to have originated there. This suggests that the original population of var. *sandwicense* on Hawaii has become gradually modified into the group now known as ssp. *St.-Johnii*. This suggestion is of course hypothetical, but it would explain the curious anomaly of the absence of var. *sandwicense* from its presumed place of origin, as well as the occurrence on Hawaii of forms

of ssp. *St.-Johnii* very similar to var. *sandwicense*.

On each island of the Hawaiian group independent modifications, some of which are superficially similar and have resulted in a sort of parallel evolution, have arisen in the populations. This curious phenomenon, which is characteristic of populations on some other Pacific islands as well, has been remarked on by Degener (1930: 266), who realized the independent origins of the hairy-leaved and "peach-leaved" forms on the various Hawaiian islands. Even more perplexing from the taxonomic point of view is the occurrence of reversions of characters. Thus, in tracing the character of style pubescence in the Polynesian species, we find that it is present in *M. rapense*, beginning to disappear in *M. Stokesii*, absent in ssp. *Wilderi*, but reappearing in ssp. *St.-Johnii*. Naturally this sort of behavior of morphological characters introduces great hazards in classifying and interpreting the phylogeny of the Polynesian species.

It is interesting that there seems to be little evidence of inter-varietal hybridization in the Hawaiian Islands. No indubitably hybrid specimens have been seen except possibly from the island of Hawaii, and here additional field work will be necessary to establish the actual hybrid nature of such specimens. The conclusion seems inevitable that evolution in Hawaiian *Myoporum* has been most strongly conditioned by geographical isolation, while inter-varietal hybridization has not played an important part. The fast rate of differentiation and slow dispersal rate of the populations have been acting together to produce an intense microevolution. The taxonomic difficulty of characterizing *M. sandwicense* is a reflection of the rapidity and recentness of this process. Within this one species can be found groups at all stages of differentiation—from individual variants to populations of almost specific distinctness.

Owing to the ruination of much of the flora of the Austral Islands, our knowledge of the groups there is rather incomplete. Nevertheless, it is clear that *M. rapense* is very closely related to *M. laetum* of New Zealand and is no doubt derived from it or a similar type. On Rapa and Tubuai it has changed little from the original immigrant, but on Raivavae it has given rise to and been almost supplanted by the polymorphic *M. Stokesii*, which itself is undergoing incipient speciation in the manner of *M. sandwicense*.

SYSTEMATIC TREATMENT

It is not pretended that the taxonomic arrangement which follows is definitive. Further collecting on some of the Hawaiian Islands may necessitate a reappraisal of some of the unnamed forms listed herein and should result in the discovery of additional forms and perhaps even new varieties. Adequate understanding of a highly polymorphic genus such as *Myoporum* requires accurate field observations, and careful notes by collectors concerning flower color and scent, fruit color, and leaf variation will be of great assistance in future studies.

MYOPORUM Soland. ex Forst. f., Prodr. 44. 1786.

Generic synonyms pertinent to the Polynesian species are:

Pentacoelium Sieb. & Zucc., Abh. Akad. Muench. 4(3): 151. 1846.

Polycoelium A. DC., Prodr. 11: 705. 1847.

Prinastrum Nutt. ex Gray, Am. Acad. Sci. 6: 53. 1866 (as synonym).

Low or erect shrubs, rarely tall trees. Leaves alternate (rarely opposite), sessile or with a winged petiole, linear to lanceolate or elliptic, entire or serrate, glabrous or rarely pubescent, often viscid when young. Flowers axillary, solitary or clustered, ebracteolate-pedicellate; calyx usually deeply 5-lobed, green and herbaceous, gland-dotted. Corolla usually 5-lobed, imbricate in the bud, subactinomorphic, campanulate to funnelform,

glabrous without, glabrous or pubescent within, usually glandular-punctate. Stamens usually 4, rarely more, alternate with the corolla lobes; filaments subulate or terete, glabrous or pubescent, adnate to the corolla; anther sacs confluent. Ovary of various shapes, often conic-cylindric, usually 2–5-celled (rarely the cells more numerous); style simple, usually as long as or longer than the ovary; stigma convex, entire or obscurely 2–5-grooved (rarely bifid); ovules solitary or rarely paired in each cell of the ovary, anatropous, pendent from the apex of the cell. Fruit a fleshy drupe; endocarp bony, usually more or less subglobose but sometimes depressed or laterally compressed; seeds spindle-shaped, with scanty endosperm, the radicle superior.

TYPE SPECIES: *Myoporum laetum* Forst. f., here chosen as lectotype for the genus. It should be noted that Forster attributed the authorship of the genus *Myoporum* to Solander alone, and not to Banks and Solander, as subsequent writers have incorrectly done.

Section PENTACOELIUM (Sieb. & Zucc.) A. Gray, Proc. Am. Acad. Sci. 6: 51–52. 1866.

Pentacoelium Sieb. & Zucc., Abh. Akad. Muench. 4(3): 151. 1846 (as a genus).

Polycoelium (A. DC.) A. Gray, *op. cit.* (as a section).

Eumyoporum Bentham, Flora Australiensis 5: 2. 1870 (as a section).

Insularia Kraenzlin, Fedde Repert. Sp. Nov., Beih. 54: 15–16. 1929 (as a section).

Ovary mostly 2–4-celled; ovule, one in each cell. Drupe mostly subglobose, not strongly laterally compressed.

KEY TO THE POLYNESIAN SPECIES

This key is intended for use in determining specimens in flower and fruit. Sterile twigs from the base of a plant or from a wounded branch may sometimes have serrate and/or densely pubescent leaves very unlike the normal ones. Specimens of this unusual type should be accompanied by normal flowering branches if the correct determination is to be made.

A. Style glabrous, or if hirsutulous then 2–3.5 mm. long and fruit not red-tinged... 1. *M. sandwicense*
  B. Style glabrous.
    C. Stamens usually 5 (less commonly 4 or 6); corolla glabrous or pubescent; leaves various, not elliptic-spatulate and abruptly acute..... 2. ssp. *sandwicense*
    D. Leaves glabrous.
      E. Endocarp strongly depressed, not or scarcely ridged, the thick wall exceeding the cells in diameter.... 5. var. *lanaiense*
      E. Endocarp of various shapes, often ridged, rarely strongly depressed, and then the wall thinner than the cells in diameter.
        F. Calyx lobes mostly 1–3 mm. long; corolla often pubescent within; style mostly 1.5–3 mm. long; drupe always greenish-white; endocarp 2–6 mm. long, 4–10-celled..... 3. var. *sandwicense*
        F. Calyx lobes mostly 3–5 mm. long; corolla glabrous (or rarely sparsely pubescent) within; style mostly 3–5 mm. long; drupe sometimes pink or purplish; endocarp 5–10 mm. long, 4–6-celled..... 4. var. *Fauriei*
    D. Leaves pubescent.
      G. Hairs branched; branchlets pubescent; leaves lanceolate or elliptic-lanceolate.. 6. var. *stellatum*
      G. Hairs unbranched.
        H. Branchlets glabrous; leaves often broadly elliptic, entire or remotely serrate.. 7. var. *Degeneri*
        H. Branchlets usually pubescent; leaves lanceolate.
          I. Corolla not over 6 mm. long; style less than 3 mm. long..... var. *sandwicense*, pubescent form
          I. Corolla over 6 mm. long; style 3 mm. long or more..... var. *Fauriei*, pubescent form
    C. Stamens constantly 4; corolla densely pubescent; leaves elliptic-spatulate, abrubtly acute.. 9. ssp. *Wikleri*
  B. Style hirsutulous; flower parts mostly 6–8; endocarp usually 7–12-celled, often sharply ridged.. 8. ssp. *St.-Johnii*
A. Style hirsutulous (rarely glabrate in *M. Stokesii*), 4–6 mm. long; stamens 4; fruit pink or red; endocarp 3–6-celled.
  J. Leaves entire; endocarp angled... 10. *M. Stokesii*
  J. Leaves serrate; endocarp not or scarcely angled. 11. *M. rapense*
    K. Calyx lobes not ciliate..... 12. var. *rapense*
    K. Calyx lobes ciliate..... 13. var. *Skottsbergii*

1. **Myoporum sandwicense** A. Gray, Proc. Am. Acad. Sci. 6: 52–53. 1866.

Polycoelium sandwicense A. DC., Prodr. 11: 706. 1847 (illegitimate name).

Usually much-branched shrubs 1–3 m. high, but stature varying from prostrate (littoral form) to trees 15 m. tall. Stem usually glabrous with smooth green or olive-brown bark when young, gray and cracking into chunks when older. Leaves alternate, often lanceolate but varying from linear-lanceolate to ovate, acute to long-acuminate, entire or often crenate or serrate, decurrent-petiolate, 3.5–22 cm. long, 0.5–4 cm. wide; usually somewhat fleshy but varying from submembranous to stiff-coriaceous when dry; usually glabrous or more rarely pubescent. Flowers axillary, in clusters of 2–10, often 1 or more abortive; pedicels terete or flattened, 0.5–1.7 cm. long. Calyx lobes 4–9, mostly 5, 1–6 mm. long, broadly ovate to oblong or lanceolate, green and herbaceous or slightly scarious on the minutely glandular-denticulate margins, glandular-punctate, usually glabrous. Corolla 4–9- (mostly 5-) lobed, 4.5–12 mm. long, campanulate to funnelform, usually glandular-punctate, entirely glabrous to densely pubescent within; color pure white, white with pink-purplish splotches, or entirely pink; corolla lobes ovate-deltoid to oblong, emarginate, obtuse, or apiculate, 2–7 mm. long. Stamens inserted on the corolla, the same number as and alternate with the corolla lobes or occasionally 1 or 2 fewer; filaments flattened-subulate, 1.5–5 mm. long; anthers 0.5–1.5 mm. long, the cells confluent by a common suture and thus changing from parallel to widely divergent at anthesis. Ovary cylindric-conic to depressed-conic, 1.5–4 mm. long, glabrous, green, 4–12-celled, the base with a yellow or purple apparently nectariferous ring; style terete or flattened, 1.5–6 mm. long; stigma convex, obscurely 2–5-grooved. Drupe fleshy, the exocarp greenish-white or creamy-white, rarely pinkish or purplish; endocarp 2–10 mm. long, 2–9 mm. broad, smooth or ribbed, subglobose or variously flattened, hard and bony when mature. Seeds one in each cell, spindle-shaped, papery when dry, 2–2.5 mm. long.

The name *Myoporum sandwicense* dates from its use by Asa Gray in 1866, the original combination *Polycoelium sandwicense* A. DC. being illegitimate under the International Rules of Botanical Nomenclature, Article 60 (1). The generic name *Polycoelium* was a substitution for the earlier *Pentacoelium* of Siebold and Zuccarini, and hence was superfluous when published. According to Article 69 of the rules, Gray's adoption of the epithet *sandwicense* is treated as a new name and not as a new combination.

As here construed *M. sandwicense* embraces three rather diverse subspecies, each of which could well be treated as a species if their differences were constant. I have been reluctant to reduce *M. Wilderi* to a subspecies, but if this were not done consistency would demand the elevation of ssp. *St.-Johnii* to specific rank, and this action does not seem warranted.

2. **Myoporum sandwicense** ssp. **sandwicense**.

Myoporum sandwicense A. Gray, Proc. Am. Acad. Sci. 6: 52–53. 1866 (in part, excluding reference to *Douglas* collection).

Prostrate shrubs to tall trees. Leaves mostly lanceolate, less commonly almost linear or ovate or elliptic, never spatulate, 3.5–22 cm. long, 0.5–4 cm. broad, glabrous or pubescent. Flowers in clusters of 2–10 (mostly 3–5). Calyx mostly 5-lobed, lobes broadly ovate to oblong or lanceolate, 1–5 mm. long. Corolla mostly 5-lobed, glandular-punctate, glabrous or pubescent within, 4.5–12 mm. long. Stamens isomerous with the corolla lobes, the fifth one occasionally reduced or absent. Ovary 4–10-celled, 1.5–4 mm. long; style glabrous, 1.5–6 mm. long. Drupe creamy- or greenish-white or rarely pinkish or purplish;

endocarp 2–10 mm. long, 2–9 mm. broad, subglobose to depressed.

This extremely variable and complex subspecies is restricted to the Hawaiian Islands.

3. **Myoporum sandwicense** ssp. **sandwicense** var. **sandwicense**.
Pls. I, 2–6; II, 16–17, 27–30; III, 38–40

Myoporum sandwicense A. Gray, Proc. Am. Acad. Sci. 6: 52–53. 1866 (in part, excluding reference to *Douglas* and *Nuttall* collections).

Leaves mostly lanceolate to oblong or ovate lanceolate, rarely sublinear or ovate, 4–22 cm. long, 0.5–3.8 cm. broad, glabrous (except in one form). Flowers in clusters of 2–9 (mostly 3–6); pedicels 0.3–1.5 cm. long. Calyx mostly 5-lobed (rarely the lobes 4, 6, or 7); lobes broadly to narrowly ovate or oblong, 1–3 (rarely 4) mm. long. Corolla 5-lobed (rarely the lobes 6–7), glandular-punctate, glabrous or pubescent within, 4.5–8 (rarely to 9.5) mm. long. Stamens usually 5, occasionally one reduced (more rarely the number 4 or 6–8). Ovary 4–10-celled but mostly 5–7-celled; style 1.5–3 (rarely 4) mm. long. Drupe creamy-white, never pink or purplish; endocarp 2–6 (rarely 7) mm. long, mostly subglobose or top-shaped, usually ribbed.

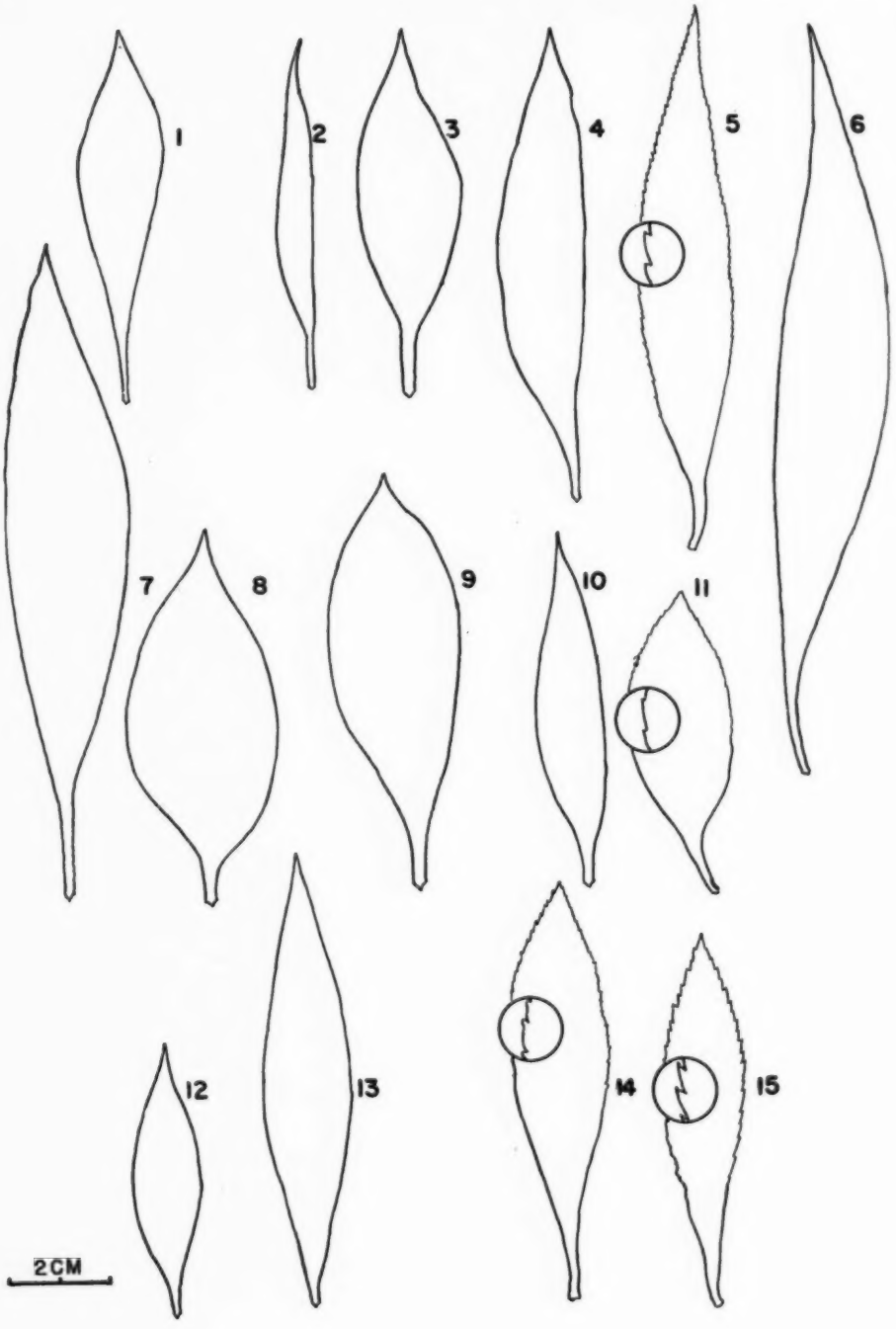
LECTOTYPE: Isles Sandwich, Oahu, *Remy 462* in the Gray Herbarium.

This extremely polymorphic variety is found at present on all the main islands except Hawaii and Kahoolawe. It is the heterogeneous residuum which remains after the more well-marked populations have been removed, and some of the forms enumerated here may warrant reappraisal when better known.

It has seemed best to arrange the various forms in a geographic sequence, first for the sake of convenience and also because forms from different islands which appear morphologically similar are most likely related not to each other but to adjacent forms on the same island. To give an idea of the correspondence and relationships of the forms, however, the following key is submitted with the caution that a clear differentiation of the forms is not possible.

Key to forms of var. *sandwicense*

A. Leaves all serrate, glabrous; style mostly 3–4 mm. long ..... Molokai Form 3
A. Leaves entire or occasionally serrate or pubescent and sharply serrate; style usually not over 3 mm. long.
B. Leaves glabrous.
C. Stamens 4; style mostly 2.5–4 mm. long ..... Oahu Form 5, Kauai Form 4
C. Stamens mostly 5, rarely more.
D. Style 2.5–4 mm. long; corolla glabrous, broadly campanulate, the lobes 5–7 ..... East Maui Form
D. Style mostly 1–3 mm. long; corolla often pubescent, the lobes mostly 5.
E. Corolla lobes 6–8, corolla pubescent ..... Oahu Form 4
E. Corolla lobes mostly 5, rarely 6.
F. Leaves large, 8–22 cm. long, often serrate; style 2–3 mm. long; corolla pubescent ..... Kauai Form 1
F. Leaves smaller, 5–14 cm. long, mostly entire; corolla glabrous or pubescent.
G. Endocarp strongly depressed.
H. Calyx less than 2 mm. long ..... Oahu Form 3
H. Calyx over 2 mm. long ..... West Maui Form 2
G. Endocarp more or less isodiametric, or at least not depressed.
I. Leaves linear-lanceolate, 8–10 times as long as broad; calyx 2–3 mm. long ..... Molokai Form 2
I. Leaves mostly less than 8 times as long as broad.
J. Leaves broadly elliptic.
K. Leaves rather membranous ..... Kauai Form 3
K. Leaves fleshy, leathery when dry ..... Oahu Form 1
J. Leaves mostly lanceolate.
L. Leaves long-attenuate ..... Kauai Form 4
L. Leaves acute to acuminate.
M. Cells of drupe 4–5; corolla mostly about 5 mm. long ..... Molokai Form 1
M. Cells of drupe mostly 5–7, less commonly 8 or more, rarely 4; corolla often longer than 5 mm. ..... Niihau Form, Kauai Form 2, Oahu Form 2, Lanai Form, West Maui Form 1
B. Leaves mostly densely pubescent and serrate, sometimes glabrous entire leaves on the same plant ..... Molokai Form 4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Specimens examined

HAWAIIAN ISLANDS (without specific locality):

Bennett (K); *Gaudichaud 39* (G-DEL, P); 1839, *Gaudichaud* (G-DEL); *Macrae* (K); *Menzies* (K); *Wilkes Expedition* (NY); "Hawaii," *Wilkes Expedition* (NY).

NIIHAU:

At foot of plateau, South East, *Stokes* (BISH, NY); south corner of plateau, *Stokes* (BISH); Kalaalaau Valley, alt. 50 ft., *St. John 22747* (BISH); Mokouia Valley, alt. 500 ft., *St. John 23592* (BISH); Paniau, 1 mile S. of, crest of windward cliff, alt. 1,200 ft., *St. John 23603* (BISH).

KAUAI:

Form 1. Leaves large, 8–22 cm. long, tending to be serrate. Stamens 5.

Waimea, seacoast, *Mann & Brigham 585* (in part) (G-BOIS, GH, NY); Waimea, Polihale, flat back of beach, *St. John et al. 22956, 22957, 22961* (BISH, T).

Form 2. Leaves mostly smaller and entire, 5.5–14 cm. long. Stamens 5.

Without locality, *Menzies* (GH); *Wawra* (G-DEL); *Wawra 2072, 2407* (W); Oct. 1916, *Rock* (BISH). Waimea, seacoast, *Mann & Brigham 585* (in part) (BISH, GH); Napali Coast, at top of beach west of Kalalau Valley, *St. John et al. 23208* (BISH, T); barren ridge, Waimea Drainage Basin, West Side, *Forbes 982.K* (BISH); Waimea, Milolii Ridge, on bare windswept headland, *St. John & Fosberg 13711* (BISH); Waimea, Polihale, rocky lowland, alt. 30 ft., *St. John et al. 22955* (BISH, T); Haeleele Valley, *Degener 9736* (DEG); northwest side of Waimea Canyon, along ditch trail at 3,500 ft., *Degener 20515* (DEG); Waimea, Kumuwela [Kumuweia] Ridge, bottom of gulch near stream, alt. 3,500 ft., *St. John, Fosberg, & Oliveira 13852* (BISH); southeast side Kumuwela Ridge, moist open forest, alt. 1,100 m., *Fosberg 12650* (BISH); Kaholuamanu, *Forbes 319.K* (BISH); same locality [Kaholuamano], *Rock? 92* (BISH), *Rock 2478* (BISH, GH, NY), *5258* (BISH), 5259 (GH).

Form 3. Leaves elliptic, rather abruptly contracted to the tip.

Without specific locality, *Remy 463* (GH).

Form 4. Like Form 2 but stamens 4.

Without specific locality, *Wawra 2299* (W).

Form 5. Leaves attenuate-acuminate, entire. Stamens 5. Drupe 6–7 mm. long.

Without locality, *Brodie* (BISH); ridge west of the Hanapepe River, *Heller 2452* (BISH, G-BOIS, G-DEL, GH, NY, P).

OAHU:

Form 1. Leaves fleshy, elliptic, up to 3 cm. wide (probably a mere ecological form).

Without locality, *Remy 461* (GH, P); Mokuleia, near sea, *Degener 9730* (DEG, NY); Moku Manu I. (islet off Mokapu Point), *Munro* (BISH).

Form 2. Leaves lanceolate. Stamens 5 or rarely 4 or 6. Drupe subglobose, 5–8-celled (up to 10-celled in specimens from Koolau Range). Styles mostly 1.5–2.0 mm. long.

Without locality: *Beechey Expedition* (G-DEL, K), *Remy 462* (GH), *Wilkes Expedition* (GH).

Waianae Range: Kaena Pt., *Bryan* (BISH); Kaena Pt., Kuaokala, *Cowan 726* (BISH); Kaena, in front of beach, alt. 15 ft., *Cowan 732, 737* (BISH); Kaena Pt., near sea,

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PLATE I

Leaf outlines of the Polynesian species of *Myoporum*.

EXPLANATION OF PLATE

M. sandwicense var. *stellatum:* (1) from *Webster 1243*, Oahu. *M. sandwicense* var. *sandwicense:* (2) from *Forbes 148.Mo*, Molokai; (3) from *Degener 9730*, Oahu; (4) from *Fosberg 13153*, Oahu; (5) from *Degener 12184*, Molokai; (6) from *Heller 2452*, Kauai. *M. sandwicense* var. *Fauriei:* (7) from *Webster & Wilbur 1775*, Hawaii; (8) from *Rock 8335*, Hawaii. *M. sandwicense* ssp. *Wilderi:* (9) from *Wilder 781*, Rarotonga. *M. sandwicense* var. *Degeneri:* (10) and (11) from *Degener 12183*, East Maui. *M. Stokesii:* (12) from *St. John & Fosberg 15956*, Raivavae; (13) from *St. John & Fosberg 15964*, Raivavae. *M. rapense* var. *Skottsbergii:* (14) from *Cuming 1430*, Tubuai. *M. rapense* var. *rapense:* (15) from *Fosberg 11525*, Rapa.

HAWAIIAN ISLANDS ASSEMBLED

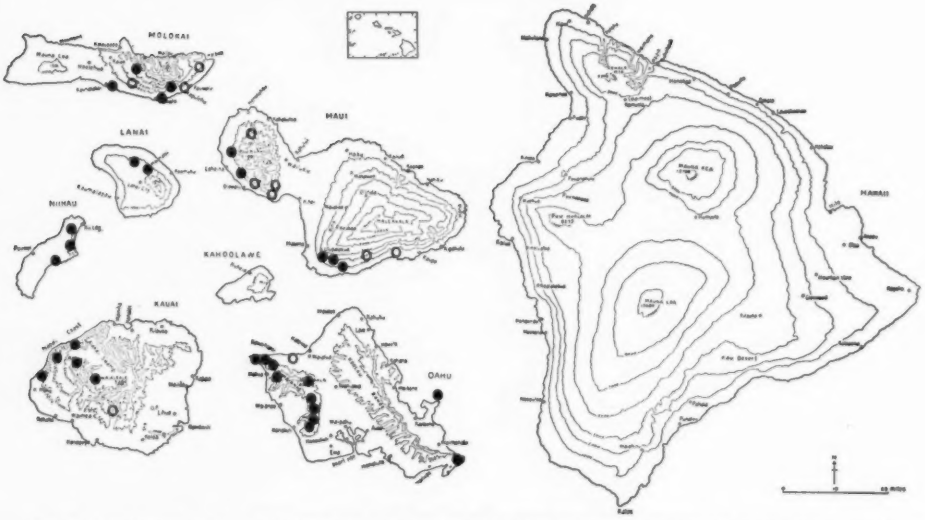


FIG. 1. Distribution of *M. sandwicense* var. *sandwicense*. Solid dots indicate exact locality, open dots approximate locality. (Base map, courtesy of Bernice P. Bishop Museum.)

Degener, Park, & Nitta 9731 (DEG); Kaena Pt., *Forbes 1652.0* (BISH, NY); bluff above Kaena Pt., alt. 60 m., *Fosberg 13153* (BISH); by railroad, Kaena Pt., alt. 15–20 ft., *Neal* (BISH); Kaena Pt., *Russ* (BISH), *Topping* (DEG); Nihoa Gulch, Mokuleia, alt. 150 ft., *Hume 307* (BISH); same locality, alt. 400 ft., *Liu* (DEG); Nihoa Gulch, Kaena, base of cliffs, alt. 400–500 ft., *St. John 11140* (BISH); near beach 1 mile east of Kaena Pt., *Webster 1077, 1079, 1080* (BISH, T), *1078* (BISH); cliffs 2 miles east of Kaena Pt., alt. 250–350 ft., *Webster 1086, 1091* (BISH, T), *1090* (BISH); at the top of the first gulch east of Kaena Pt., alt. 400 ft., *Webster 1092.A* (BISH, T), *1092.B* (near to Form 3) (BISH); cliffs 1 mile east of Kaena Pt., alt. 400 ft., *Webster & Cowan 1097* (BISH, T); near road 1 mile east of Kaena Pt., *Webster & Krauss 1096* (BISH); Kewaula Valley, arid rocky valley, *Degener, Park, & Nitta 9732* (DEG, NY); arid ravine near Kawaihapai, *Degener 2197* (DEG, NY); steep brushy wall of gulch, south side Makua Valley, alt. 500 m., *Fosberg 12350* (BISH); Mt. Kaala, forest at 2,500 ft., *Degener, Murashige, & Kerr 19736* (transitional to Form 4) (DEG); Puu Kanehoa, southeast ridge of south peak, alt. 1,900 ft., *St. John 23291* (BISH).

Koolau Range: Maunalua, Kealakipapa Valley, alt. 5 m., *Fosberg 10919* (BISH, DEG); Maunalua, east bottom of Kalama Valley, alt. 15 m., *V. O. Fosberg 93, 95* (BISH); Maunalua, head of Manuwaii Valley, alt. 180 m., *V. O. Fosberg 85* (BISH); arid rocky region west of Makapuu Head, *Degener, Park, & Hirai 9728* (DEG, G-DEL, NY); rocky lowland 1 mile southwest of Makapuu Point, alt. 10 ft., *Dunn* (BISH).

Form 3. Like Form 2 but drupe strongly depressed.

Waianae Range: cliffs 2 miles east of Kaena Pt., alt. 250–350 ft., *Webster 1081* (BISH, T); Kawaihapai Valley, alt. 400 ft., *Suehiro* (BISH).

Form 4. Like Form 2 but flower parts 6–8.

Waianae Range: Kawaihapai, arid rocky

region, *Degener, Park, & Topping 9729* (DEG, NY).

Form 5. Stamens invariably 4. Style 2–3 mm. long.

Waianae Mountains, *Hillebrand* (K); Waianae Range, *Hillebrand* (K); Kealia Trail, *Selling 3913* (transitional to Form 2) (S); same locality, steep brushy slope, alt. 300 m., *Fosberg 12858* (BISH); Puu Kaala, Waianaeuka, alt. 650 m., *Fosberg 12614* (BISH); same locality, alt. 2,000 ft., *St. John 12930* (BISH), *Webster & St. John 1501* (BISH, T); near Kolekole Pass, *Selling* (*Bog Survey*) *3914* (BISH, S); Popouwela, *Forbes 1593* (BISH, NY); Puu Kanehoa, east ridge, alt. 1,700 ft., *St. John 14065* (BISH); Lihue Gulch, east branch, *Forbes 1688.0* (BISH); same locality, *Russ* (BISH); Pouilihale ridge, semi-moist brushy ridge, alt. 700 m., *Fosberg 13782* (BISH); Palehua, Honouliuli, crest of ridge, alt. 2,000 ft., *St. John 11162* (BISH); Palehua, alt. 650 m., *Skottsberg 324* (S); near Mauna Kapu, *Degener 9741* (DEG).

MOLOKAI:

Form 1. Leaves narrowly lanceolate, entire, glabrous; drupe 4–5-celled.

Kaunakakai, below government road, on beach, *Wilder* (BISH, NY); east fork of Kawela Valley, *Degener 12181.B* (DEG); Kamalo, alt. 1,000 m., *Faurie 678* (BISH); Kamalo road, sea-level, *Rock 12578* (BISH); beach at Kamalo, *Rock 17137* (annotated by Rock with an unpublished varietal name) (BISH); Mapulo'u [Mapulehu], *Rock 6153* (GH, NY); Pukoo, *Faurie 679* (P); south slope of Halawa Valley, *Degener 9737* (DEG, G-DEL, NY).

Form 2. Leaves linear-lanceolate, entire, glabrous; drupe 5–8-celled.

Slopes of Puu Kolekole, *Forbes 148.Mo* (BISH, NY, P).

Form 3. Leaves oblong-lanceolate, all serrate, glabrous; drupe 4–5-celled.

North slope of Puu Kaeo, *Degener 9739* (DEG); above head of Waikolu Valley, rainy shrubby gully, *Degener 12182, 12184* (DEG); Waikolu, steep valley wall below Puu Kaeo, wet woods, alt. 3,000 ft., *St. John et al. 23431* (BISH); same locality, alt. 2,800 ft., *St. John et al. 23466* (BISH); same locality, alt. 2,000 ft., *St. John et al. 23441* (BISH); Manawai—Kahanui ridge, moist forest, alt. 600 m., *Fosberg 13392* (BISH).

Form 4. Leaves serrate, densely pubescent, or glabrous and entire leaves on the same plant.

Puu Kolekole, *Forbes 181.Mo* (BISH); east fork of Kawela Valley, three distinct forms growing together on dry rocky slope, *Degener 12181.A* (serrate-pubescent), *12181.C* (entire, pubescent), *12181.D* (entire, glabrous) (DEG).

LANAI:

Without specific locality, *Forbes* (BISH); flats above head of Hawaiilanui Gulch, alt. 500 m., *Fosberg 12523* (BISH); Maunalei Gulch, dry basalt talus, alt. 800 ft., *St. John, Eames, & Hosaka 18812* (BISH); Limestone Point, *Munro* (BISH) (identification doubtful).

WEST MAUI:

Form 1. Leaves narrowly lanceolate; drupe subglobose or broadly ovoid.

Without definite locality, *Mann & Brigham 387* (G-DEL, GH, NY); Lahainaluna, Aug. 1910, *Forbes* (BISH, NY); south ridge of Laniupoko Valley, alt. 1,000 ft., *St. John & Catto 17705, 17706* (BISH); Olowalu Valley, *Forbes 2325.M* (BISH, NY); from Papawai Point toward Puu Anu through Manawainui Gulch, *Degener 9742* (DEG, NY); Pohakea Gulch, arid windy slope, *Degener 9743* (DEG, G-DEL, NY); Wailuku, gulch south of Waikapuu [Waikapu] Valley, *Skottsberg 783* (BISH, S).

Form 2. Like Form 1 but drupe strongly depressed.

Honokahau [Honokohau] Drainage Basin, *Forbes 477.M* (BISH, NY, P).

EAST MAUI:

The single form is much like West Maui

Form 1 but the style is longer and the flower parts may be more than 5.

"Sandwich Islands," *Hillebrand* (probably from East Maui) (GH); East Maui, *Hillebrand* (K); Haleakala, *Hillebrand* (K); Kula, open rocky Kula land, alt. 1,000 ft., *Wilder 282* (BISH); near Ulupalakua, *Degener 9740* (DEG, G-DEL, NY); southwest slope of Haleakala, above Kanaio, *Alexander & Kellogg 5353* (BISH); Hokukano, arid lava waste, *Degener & Clay 19408* (DEG); Nakaaha, dryish lava waste, *Degener 19306* (DEG); Nuu, rough lava flow, *Forbes 1910.M* (BISH).

The forms of var. *sandwicense* range in value from those which are probably ecological modifications to those which approach varietal distinction. Oahu Form 5 was at first thought to be possibly a variety because of its flowers with only four stamens, but the specimen collected by St. John (number *23291*) from the center of its range at Puu Kanehoa shows that the stamen character is not constant.

The most perplexing forms of var. *sandwicense* are those found on Molokai, and additional field work must be done before a final systematic arrangement of them can be made. Molokai Form 3 is on the borderline of varietal status, but it is being kept as a form at present because its best character—constantly and sharply serrate leaves—does not distinguish it from populations on other islands within which serrate leaves are not uncommon.

4. **Myoporum sandwicense** ssp. **sandwicense** var. **Fauriei** (Lévl.) Kraenzlin, Fedde Repert. Sp. Nov. Beih. 54: 21. 1929.
Pls. I, 7–8; II, 18–19, 31; III, 41.

Myoporum Fauriei Lévl., Fedde Repert. Sp. Nov. 11: 63. 1912.

Leaves ovate-lanceolate to ovate or elliptic, acute or acuminate, entire or serrate, 5–17 cm. long, 0.9–4 cm. broad, mostly coarse and brittle-coriaceous but often thinner, glabrous or rarely pubescent. Flowers 2–5 to an axil;

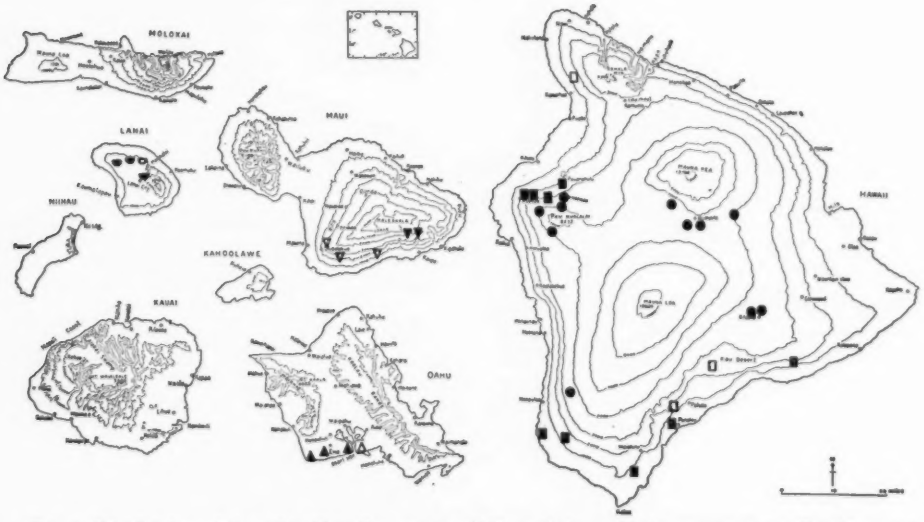


FIG. 2. Distribution of the other Hawaiian groups of *M. sandwicense*. Circles represent var. *Fauriei*, squares ssp. *St.-Johnii*, erect triangles var. *stellatum*, inverted triangles var. *Degeneri*, semicircles var. *lanaiense*. Solid symbols indicate exact locality, open symbols indicate approximate locality; specimens of really doubtful locality and those examined after the completion of this plate are not mapped. (Base map, courtesy of Bernice P. Bishop Museum.)

pedicels 0.5–1.7 cm. long. Calyx lobes 5 (rarely 6), 2.5–6 (mostly 3–5) mm. long, ovate-lanceolate to lanceolate. Corolla 5-lobed (rarely 6-lobed), 6.5–12 mm. long, glabrous or more rarely sparsely pubescent. Stamens mostly 5, rarely 6, often with one stamen reduced or sometimes entirely wanting. Ovary 2.5–4 mm. long, 4–6-celled (rarely 7-celled); style 2.5–6 (mostly 3–5) mm. long, glabrous. Drupe creamy-white or often pinkish or rarely purplish; endocarp broadly ovoid, 5–10 mm. long, not prominently ribbed.

TYPE: "Sandwich: Hawai, Maunakea, 2,000 m., juill. 1909 (Faurie, 677)." An isotype is in the Bishop Museum.

This variety is limited to the upper dry forest (altitude 4,000 feet to the timber line) on the island of Hawaii.[3] It is conspicuous because of its large leaves, flowers, and fruit and seems a distinct entity in spite of its overlap of characters with var. *sandwicense*. Usually var. *Fauriei* has longer calyx lobes, styles, and drupes than var. *sandwicense*, but this does not always hold and then characters such as the number of cells in the drupe, the lack of corolla pubescence, and the general leaf aspect of var. *Fauriei* must be considered. Var. *Fauriei* appears to be the most primitive group of ssp. *sandwicense* and closely resembles ssp. *Wilderi* in flower size and drupe characters. Its retention of the pinkish drupe color and its flowers which often lack the fifth stamen are primitive characters of special significance. Within var. *Fauriei* one finds a great deal of polymorphism, there being large and small flowers, long elliptic-lanceolate and short ovate leaves; but I have not been able to segregate these types into populations.

Specimens examined

HAWAII:

Form 1. Leaves glabrous; flower parts in 5's; cells of drupe 4–6.

"Hawaiian Islands" (no definite island cited): *Collector unknown* (BISH); Bonite voyage, *Gaudichaud* (GH); *Hillebrand* (K); *Mann & Brigham 568* (BISH).

Hawaii, without definite locality, *Challenger Expedition* (K), *Wilkes Expedition* (GH); South Hilo District, Waiakea, 22 miles up Saddle Road, alt. 5,100 ft., *St. John, Cowan, & Rogers 22391* (BISH); North Hilo District, Humuula, Puu Huluhulu, alt. 6,750 ft., *Bryan* (BISH); same locality, alt. 6,760 ft., *St. John et al. 23934, 23935* (glabrous sucker shoot from same plant as *23934*), *23936* (pubescent sucker shoot from same plant) (BISH); Humuula, Saddle Road 1 mile south of Omaokoili, south slope of cinder cone, alt. 6,650 ft., *St. John, Cowan, & Rogers 22379, 22380* (BISH); Pohakuloa, alt. 6,500 ft., *Bryan* (BISH); slopes of Mauna Kea above Waikii, *Rock 8335* (BISH, GH); Puuwaawaa, *Austin* (BISH), *Munro* (BISH); Kona, above Huehue, *Rock 3489* (BISH, GH); Hualalai, Puu Laalaau, alt. 6,300 ft., *Kondo* (BISH); Puu Hualalai, 4,100–6,500 ft. alt., *St. John et al. 11394* (BISH); Kona, Captain Cook, south of Papaloa, alt. 5,000 ft., *Degener & Murashige 20335* (DEG); Kealakekua, Greenwell Ranch, alt. 4,500 ft., *St. John & Hatheway 23982* (BISH); South Kona District, Alika Homesteads, Koa Mill, alt. 4,500 ft., *St. John et al. 22486* (BISH); Kilauea, *Forbes ?* (BISH), *Forbes, Brigham, & Thompson* (BISH, P); Hawaii National Park, Kipuka Ki, alt. 4,300 ft., *Webster & Wilbur 1702, 1703, 1704, 1705, 1706, 1707* (BISH, T); Hawaii National Park, Bird Park [Kipuka Puaulu], alt. 4,000 ft., *Degener 9735* (DEG, NY); same locality, *Bog Survey 3254* (S), *Eastwood* (NY), *St. John et al. 11260, 11266* (BISH), *Setchell* (S), *Skottsberg 541* (BISH, S), *Webster & Wilbur 1775, 1776, 1777* (BISH, T).

Form 2. Leaves pubescent; flower parts in 5's; cells of drupe 4–6.

North Hilo District, Humuula, Puu Huluhulu, open woods on cinder hill kipuka, alt. 6,570 ft., *St. John et al. 23944* (BISH).

[3]Kraenzlin (1929: 21) erred in referring a collection from the New Hebrides (Herb. Boissier) to this variety. I have seen the material, and although it is too fragmentary to determine positively, there is no reason to believe that it represents *M. sandwicense*.

Form 3. Leaves pubescent; flower parts 6–7; cells of drupe 7–9.

Puuwaawaa, *Rock 3800* (BISH, NY). In several respects this form is intermediate between var. *Fauriei* and ssp. *St.-Johnii*.

5. **Myoporum sandwicense** ssp. **sandwicense** var. **lanaiense** Webster, var. nov.

Pls. II, 21, 33; III, 43

Drupa depressi-conica; endocarpium non costatum.

Leaves lanceolate, acuminate, entire, glabrous, 6–13.5 cm. long, 0.8–1.8 cm. wide. Flowers 2–4 per axil; pedicels 0.7–1 cm. long. Calyx lobes 5, 2–3 mm. long, ovate-acuminate. Corolla 5-lobed, 5–8 mm. long, glabrous or pubescent, the tube 2.5–4 mm. long. Ovary about 2 mm. long; style 1.8–3 mm. long. Drupe probably whitish in color; endocarp depressed-conic or hemispheric in outline, not or scarcely ridged, 3–4.5 mm. high, 6–9 mm. broad, 5–7-celled.

TYPE: Mahana forehills, Lanai, July 1910, *Rock 8119*, in the Bishop Museum Herbarium. Isotypes are in the Gray Herbarium and Naturhistorisches Museum, Vienna.

This variety, named for the island on which it occurs, is apparently now restricted to the dry forest near Kanepuu at the northwest end of the island. Ordinarily it is easily distinguished from var. *sandwicense* by its strongly depressed endocarp. Rarely, plants of var. *sandwicense*, such as *Webster 1081* from Oahu and *Forbes 477.M* from Maui, may have depressed endocarps which appear superficially similar, but these are easily distinguished in cross section by their thinner walls (compare Figs. 39 and 43).

The status of var. *sandwicense* on Lanai is rather uncertain. Judging from the few collections at hand, it seems to occupy a lower altitudinal zone than var. *lanaiense*, but further collecting will be necessary before its distributional relationship to var. *lanaiense* will become clear.

Specimens examined

LANAI:

Koa dry forest, Lanai, *Munro 61* (BISH, NY); plateau on lee side of island, alt. 600 m. (?), *Wilder 90* (BISH); xerophytic forest near Kanepuu, *Fosberg 12551* (BISH); Kanepuu, Kaa, alt. 1,600 ft., *St. John, Eames, & Hosaka 18803* (BISH); same locality, alt. 1,700 ft., *St. John & Cowan 22624* (BISH); flats above head of Hawaiilanui Gulch, alt. 500 m., *Fosberg 12525* (BISH); Poomai [=Paoma?], *Munro* (BISH); Mahana Valley, *Munro 171½* (BISH); Mahana forehills, *Rock 8119* (BISH, GH, W); mountains near Koele, *Forbes 91.L* (BISH).

6. **Myoporum sandwicense** ssp. **sandwicense** var. **stellatum** Webster, var. nov.

Pls. I, 1; II, 20, 32; III, 42

Prinastrum cauliflorum Nutt. ex Gray, Am. Acad. Sci. 6: 52. 1866 (herbarium name published in synonymy).

Folia hirtella, ramuli hirtelli; pili ramosi.

Branchlets and leaves pubescent with branched hairs, somewhat glabrescent with age; leaves elliptic-lanceolate, usually entire, 4–9 cm. long, 0.7–2.2 cm. broad. Calyx mostly 5-lobed, pubescent, sepals 1.2–2.5 mm. long. Corolla 5-lobed (rarely 6-lobed), 5–7 mm. long, glabrous or pubescent within, the glandular dots rather inconspicuous. Stamens mostly 4 or 5, if 5 then often one reduced. Ovary 2–2.5 mm. long; style 2–2.8 mm. long. Drupe creamy-white; endocarp subglobose, ridged, 3–5 mm. in diameter, 5–7-celled.

TYPE: Oahu, Ewa coral plain near Barbers Point, alt. 10 ft., *Webster 1243*, in the Bishop Museum Herbarium (isotype in the University of Texas Herbarium).

This distinctive variety is now restricted to the low plain of emergent coral at the southwestern corner of Oahu. It is known from Kauai on the basis of a single collection by Nuttall, but has not been collected on that island in the century since then. If Nuttall's rather questionable locality was correct, the variety has evidently become extinct on

Kauai. On Oahu it originally grew from the mouth of Pearl Harbor to Barbers Point, but it has been exterminated over much of this range by the encroachment of military establishments. In the vicinity of the lighthouse it is still quite abundant, however, and will continue to persist unless the vegetation is entirely removed. Ecologically, it must be highly specialized, as it has become adapted to a calcareous substrate quite different from the lateritic or basaltic soils on which the other varieties grow.

Although this variety superficially resembles var. *Degeneri* in the pubescent leaves, it has been independently derived, probably from Oahu Form 5 of var. *sandwicense*. This relationship is especially evident in the fact that var. *stellatum* shows the tendency toward the loss of the fifth stamen which is fully expressed in the form from the Waianae Range.

The name of this variety alludes to the appearance of the branched hairs, a character unique in the genus as far as I can determine.

Specimens examined

KAUAI:

Atooi [=Kauai], *Nuttall* (K).

OAHU:

Honouliuli, Barbers Point coral plain, alt. 10 ft., *Cowan 787, 788* (BISH); same locality, *Degener & Park 9727* (DEG), *Egler 37–268* (BISH), *Hosaka 1359* (BISH), *Pollock* (*F. Brown's*) *1278* (BISH), *Rock 17038* (BISH, labeled with an unpublished varietal name), *Setchell* (GH), *Webster 1243, 1244, 1250* (BISH, T), *1245* (BISH), *1249* (T); between Barbers Point and Pearl Harbor, along beach, *Degener & Park 9733* (DEG); Ewa, below Magnetic Observatory toward beach, *Egler & Hosaka 37-419* (BISH); Puuloa, 1909, *Stokes* (BISH); east side of Pearl Harbor, *Stokes* (BISH).

7. **Myoporum sandwicense** ssp. **sandwicense** var. **Degeneri** Webster, var. nov.
Pl. I, 10–11

Folia elliptica hirtella serrata; pili simplici; ramuli glabri.

Branchlets glabrous. Leaves mostly elliptic, less commonly lanceolate, pubescent, the hairs unbranched, entire or serrate, 4–9 cm. long, 1–2.5 cm. broad. Flowers 5–6 per axil. Calyx lobes 5, glabrous or pubescent, 1.5–3.5 mm. long. Corolla glabrous or pubescent within, 5–7.5 mm. long. Stamens 5, rarely 4 or 6. Ovary 2–3.5 mm. long; style 2–5 mm. long. Drupe color unknown, presumably white; endocarp 5–9 mm. long, 5–7-celled.

TYPE: East Maui, north mauka of Ulupalakua, *Degener 12183*, in the Bishop Museum Herbarium.

This variety occurs on the dry leeward slopes of Haleakala, East Maui, from near Ulupalakua to the Kaupo Gap; a form from Molokai is referred here for convenience. It is named for Mr. Otto Degener, long a student of the Hawaiian *naio*, who illustrated it in his book, *Plants of Hawaii National Park*.

Specimens examined

MOLOKAI:

Probably near Kaluaaha, *Degener 9738* (DEG, NY).

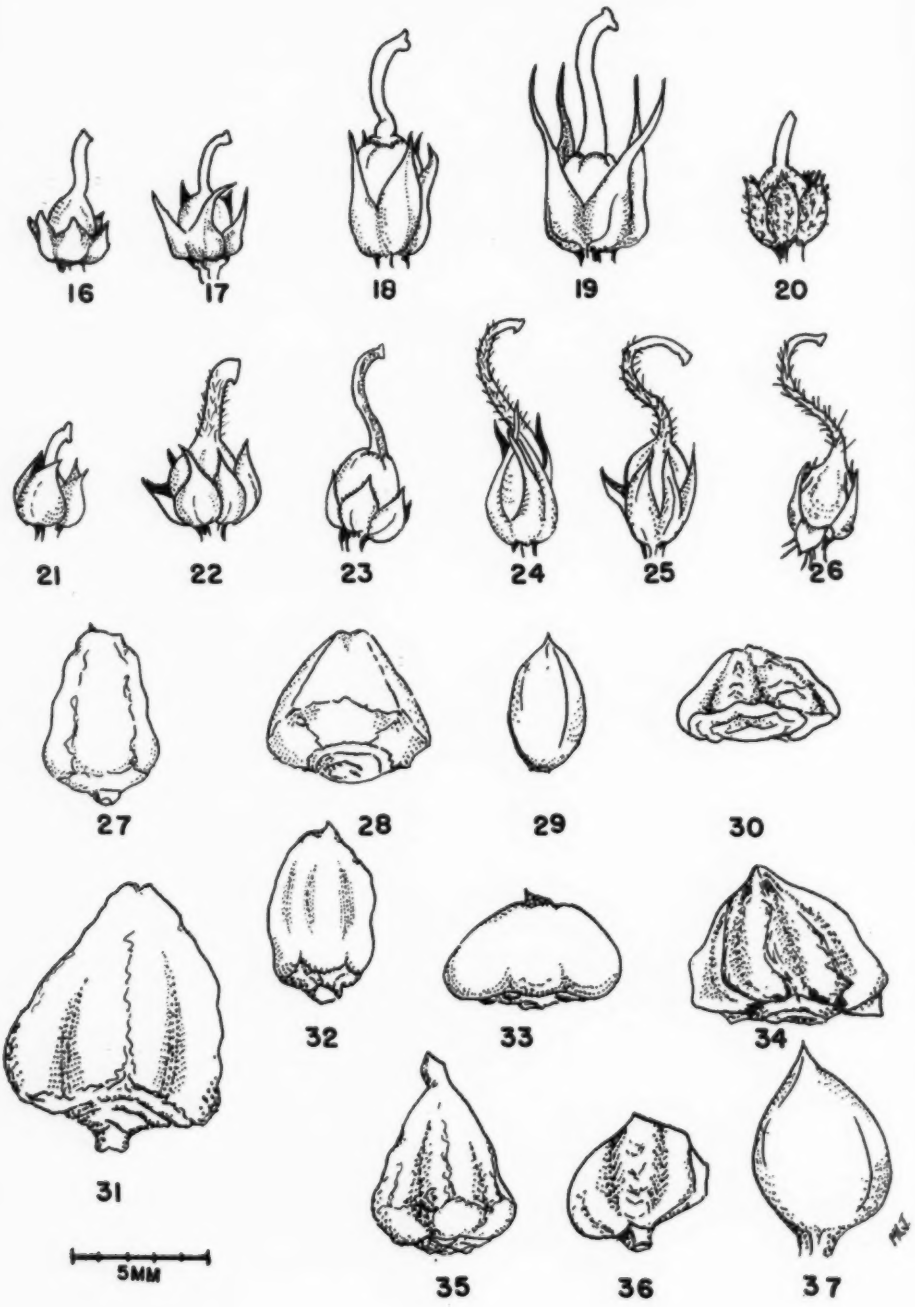
EAST MAUI:

North mauka of Ulupalakua, *Degener 12183* (BISH, DEG); Auhi [=Auwahi], Ulupalakua, *Munro 385* (BISH); Kaapilopilo and Kapakahawai gulches, *Forbes 1940.M* (BISH); Waiopaa [=Waiopai] Ranch, *Forbes 1875.M* (BISH); Haleakala, Kaupo Gap, *Forbes 1105.M* (BISH); Haleakala, south of Kuiki along east side of Kaupo Gap, *Degener 17600* (NY).

Although the plant from Molokai is placed in var. *Degeneri* for convenience, it probably has arisen independently of the Maui plants and may represent a different variety. However, until the confusing forms from Molokai are better understood, it seems unwise to describe any new varieties from there.

8. **Myoporum sandwicense** ssp. **St.-Johnii** Webster, ssp. nov.
Pls. II, 22, 34–35; III, 44

Petala et sepala plerumque 6–8; stylus hirtellus; drupa plerumque 7–12-locularis.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Shrubs to small trees, 2–8 m. high. Leaves mostly oblong-lanceolate, entire, glabrous, 4–15 cm. long, 0.5–3 cm. broad. Flowers 3–8 per axil; pedicels 0.6–1.2 cm. long. Flower parts varying from 5–9 but mostly 6–8, the sepals equal to or less than the number of corolla lobes. Sepals 1–3 mm. long. Corolla 5–8.5 mm. long, usually densely pubescent within, gladular spots absent or very few. Stamens usually 5–9 (very rarely less than 5), the same number as or less than the number of corolla lobes. Ovary 2–3 mm. long; style hirsutulous, 1.7–3.5 (mostly 2–3) mm. long. Drupe creamy-white; endocarp usually strongly ridged, more or less laterally compressed, 3–8 mm. long, 3.5–8 mm. broad, 5–13-celled but typically 7–12-celled.

TYPE: Hawaii, Kaupulehu, 2–3 miles east of Huehue, alt. 2,000 ft., *Webster & Wilbur 1835*, in the Bishop Museum Herbarium (isotype in the University of Texas Herbarium).

This polymorphic subspecies is restricted to the lower dry forests on the island of Hawaii. In its possession of a hirsutulous style it is unique among the groups within *M. sandwicense*, and it is further well marked by its large number of perianth parts, reduction of glandular spots on the corolla, and many-celled, sharply ribbed, endocarp. Morphologically, the typical form (Form 1) is fully as distinct from the other varieties of *M. sandwicense* as many species of this genus are from one another. But the typical form intergrades with Form 2, which may be almost indistinguishable from some forms of var. *sandwicense*. This is especially true of specimens from the vicinity of Punaluu in the Kau District, but because they occur in the same area as plants of Form 1 and apparently are intermixed with them, it seems preferable to regard them as merely aberrant individuals of ssp. *St.-Johnii*, which for some reason (possibly they are remnants of an ancient population of var. *sandwicense* ?) are especially common in this vicinity.

This group is named for Dr. Harold St. John of the University of Hawaii, who suggested the study of *Myoporum* and whose assistance has greatly helped to overcome the disadvantages of completing this work at a distance from the Hawaiian Islands.

Specimens examined

HAWAIIAN ISLANDS (without specific locality):

Douglas 21 (K), *Douglas* (W).

HAWAII:

Form 1. Style hirsutulous and flower parts mostly 6–8. Cells of endocarp 7–13.

North Kona, *Alexander & Kellogg 5367* (BISH); vicinity of Huehue near main road, *Bog Survey 3213* (BISH, S); between Puuwaawaa and Huehue, *Degener 2210* (DEG); Puuwaawaa, *Degener 9726* (DEG, NY), *Nishina (Degener's) 9744* (DEG, NY); 2.3 miles northeast of Huehue Ranch House, Kaupulehu, alt. 2,000 ft., *St. John et al. 22525* (BISH);

PLATE II

Reproductive structures of the Polynesian species of *Myoporum*.

EXPLANATION OF PLATE

Mature pistils (FIGS. 16–26).

M. sandwicense var. *sandwicense:* (16) from *Webster 1097*, Oahu; (17) from *Heller 2452*, Kauai. *M. sandwicense* var. *Fauriei:* (18) from *Webster & Wilbur 1706*, Hawaii; (19) from *Webster & Wilbur 1702*, Hawaii. *M. sandwicense* var. *stellatum:* (20) from *Degener 9727*, Oahu. *M. sandwicense* var. *lanaiense:* (21) from *Rock 8119*, Lanai. *M. sandwicense* ssp. *St.-Johnii:* (22) from *Webster & Wilbur 1835*, Hawaii. *M. sandwicense* ssp. *Wilderi:* (23) from *Wilder 781*, Rarotonga. *M. Stokesii:* (24) from *St. John & Fosberg 15947*, Raivavae. *M. rapense* var. *rapense:* (25) from *St. John & Fosberg 15280*, Rapa. *M. rapense* var. *Skottsbergii:* (26) from *Cuming 1430*, Tubuai.

Side view of endocarps (FIGS. 27–37).

M. sandwicense var. *sandwicense:* (27) from *St. John et al. 23208*, Kauai; (28) from *Degener 9729*, Oahu; (29) from *Degener 9737*, Molokai; (30) from *Forbes 477.M*, West Maui. *M. sandwicense* var. *Fauriei*: (31) from *Webster & Wilbur 1706*, Hawaii. *M. sandwicense* var. *stellatum:* (32) from *Degener 9727*, Oahu. *M. sandwicense* var. *lanaiense:* (33) from *Rock 8119*, Lanai. *M. sandwicense* ssp. *St.-Johnii:* (34) from *Webster & Wilbur 1835*, Hawaii; (35) from *Degener 2211*, Hawaii. *M. Stokesii:* (36) from *Fosberg 11784*, Raivavae. *M. rapense* var. *rapense:* (37) from *St. John & Fosberg 15280*, Rapa.

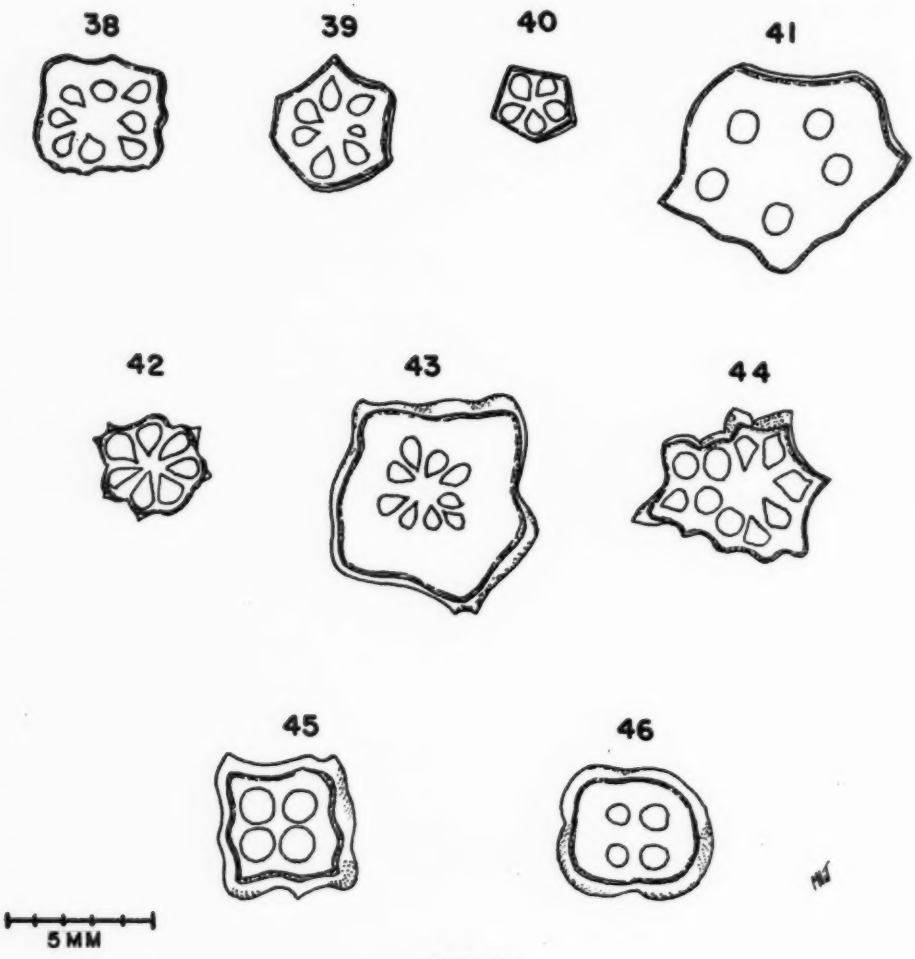

PLATE III

Reproductive structures of the Polynesian species of *Myoporum*.

EXPLANATION OF PLATE

Endocarps in cross section.

M. sandwicense var. *sandwicense:* (38) from *V. O. Fosberg 93*, Oahu; (39) from *Webster 1081*, Oahu; (40) from *Degener 9737*, Molokai. *M. sandwicense* var. *Fauriei:* (41) from *Webster & Wilbur 1704*, Hawaii. *M. sandwicense* var. *stellatum:* (42) from *Degener 9727*, Oahu. *M. sandwicense* var. *lanaiense:* (43) from *Fosberg 12525*, Lanai. *M. sandwicense* ssp. *St.-Johnii:* (44) from *Webster & Wilbur 1835*, Hawaii. *M. Stokesii:* (45) from *St. John & Fosberg 15956*, Raivavae. *M. rapense* var. *rapense:* (46) from *Fosberg 11525*, Rapa.

Puuwaawaa, 4 miles southwest of Puu Anahulu, alt. 2,000 ft., *Webster & Wilbur 1874, 1883, 1895* (BISH, T); Puuwaawaa, 3 miles west of Puuwaawaa Hill, alt. 3,000 ft., *Webster & Wilbur 1852, 1857* (BISH, T); Kaupulehu, 2–3 miles east of Huehue, alt. 2,000 ft., *Webster & Wilbur 1835* (BISH, T); Keahuolu, alt. 400 ft., on aa in dry scrub, *St. John & Lane 23978* (BISH); Kapua ?, near the sea, *Bryan* (BISH); Kapua, on kipuka south of Hana-

keaumoe triangulation point, near sea level, *Bryan 761* (BISH); Manuka Mauka, alt. 750–1,750 ft., *St. John et al. 11326* (BISH); Kau, halfway between Kaalualu and Waiohinu, *Degener 9734* (DEG, NY); old aa flow, Hilea, *Russ* (BISH); Kau District, Ninole, Wailua Ninole, basalt flow near shore, alt. 15 ft., *St. John, Hatheway, & Morton 23950* (BISH); Punaluu, *Degener & Wiebke 2207* (DEG, NY); on aa flow, Punaluu, alt. 500 ft., *Neal* (BISH); Hawaii National Park, Bird Park, *Degener 9725* (DEG); Naaulu Forest, Kealakomo, alt. 1,700 ft., *Fagerlund & Mitchell 800* (BISH).

St. John et al. 23950 has the hirsutulous style typical for the subspecies but is remarkable in having the stamen number highly variable and reduced to 2–3 in the majority of flowers. The locality of *Degener 9725* should be regarded with suspicion because Bird Park has been visited many times by botanists, and only var. *Fauriei* has been collected there.

Form 2. Style very sparsely hirsutulous or glabrous; flower parts mostly 5–6; cells of endocarp 5–7.

Seventeen miles from Kohala toward Waimea, *Degener & Wiebke 2208* (DEG, NY); Puu Keekee, *Degener, Greenwell, & Murashige 20020* (DEG); 20 miles from Waimea toward Kona, *Degener & Wiebke 2211* (DEG, NY); Puuwaawaa, *Forbes 49.H* (BISH); Kau Desert 25 miles west of Kilauea, *Degener & Wiebke 2209* (G-DEL, NY); Kau District, Punaluu, *St. John et al. 11316* (BISH); same locality, *St. John, Cowan, & Rogers 22426* (BISH).

Degener, Murashige, & Greenwell 20019 (DEG), collected near Na Puukulua, is sterile and has serrate-pubescent "juvenile" leaves, but since it was found near number *20020* it probably belongs here.

9. **Myoporum sandwicense** ssp. **Wilderi** (Skottsberg) Webster, comb. nov.

Pls. I, 9; II, 23

Myoporum Wilderi Skottsberg, Acta Horti Gotob. 8: 165–166. 1933.

Shrubs or small trees. Leaves spatulate-elliptic or obovate-elliptic, acute or apiculate, glabrous, entire, 5–10.5 cm. long, 1.8–3.3 cm. wide. Flowers 3–4 per axil; pedicels 0.8–1 cm. long, flattened. Calyx 5-lobed, glandular-dotted, glabrous, the lobes mostly 1.5–2 mm. long. Corolla white, 7.5–9 mm. long, glandular-spotted, pubescent within, 5-lobed. Stamens 4 (sometimes with traces of a fifth according to Skottsberg). Ovary globose-pyriform, about 3 mm. long; style 3–4.5 mm. long, curved at the base, glabrous. Drupe color unknown (probably purplish or reddish); endocarp top-shaped, about 5–6 mm. long, 4–6-celled.

TYPE: Rarotonga, *Wilder 781*, in the Bishop Museum Herbarium.

This subspecies is cultivated by the natives of Rarotonga, in the Cook Islands of southern Polynesia, and has been found in the wild state only on the nearby island of Mangaia. It is fairly well distinguished from the other two subspecies by its leaf shape and by its flowers with only 4 stamens. However, most of the characters given by Skottsberg (1933: 155) to separate *M. Wilderi* from *M. sandwicense* are not applicable when a large amount of material of the latter species is examined. Hairy corolla lobes occur in most of the Hawaiian varieties, and the density of the pubescence may be as great as in the Rarotongan plant. The constant absence of the fifth stamen in the Cook Island population seems like a good distinction, but the form of var. *sandwicense* from the Waianae Range of Oahu usually lacks the fifth stamen, and similarly reduced flowers are not uncommon in var. *stellatum* and var. *Fauriei*. The length of the style does not distinguish Skottsberg's species because the style in var. *Fauriei* reaches 5 mm. and more in length. There remains the leaf shape to fall back upon, and although this is rather distinctive in ssp. *Wilderi*—the rounded apex of the elliptic leaf being rather abruptly contracted into an apiculate tip—it is variable even on the type specimen and does not seem to be a character of specific value.

Perhaps the best distinguishing character for ssp. *Wilderi* is that its flowers have an odor so noticeable that the plant is cultivated for perfume. In this respect the subspecies resembles the strongly scented Austral Island plants and contrasts with the relatively odorless Hawaiian plants. The basal curvature of the style is another link between the Cook Island and Austral Island plants; but this character is probably dependent on the length of the style and is of no great intrinsic significance.

Specimens examined

COOK ISLANDS:

Rarotonga, *Wilder 781* (BISH, NY); Mangaia, Nov. 1928, *Graham* (BISH).

10. **Myoporum Stokesii** F. Brown, Bishop Mus. Bul. 130: 277–278, fig. 41. 1935.

Pls. I, 12; II, 24, 36; III, 45

Shrubs or trees, 1–5 m. high. Leaves elliptic-lanceolate, entire, glabrous, 3.5–9 cm. long, 0.5–1.7 cm. broad, acute, apiculate, or attenuate-acuminate, alate-petiolate. Flowers 1–3 (rarely 4) per axil, sometimes accompanied by 1 or more small abortive flowers; pedicels 0.7–1.4 cm. long. Calyx 5-lobed, glandular-dotted; calyx lobes 2–4 mm. long, entire-margined. Corolla pure white or pink-spotted in the throat, rather heavily fragrant, 9–12 mm. long, pubescent within. Stamens 4. Ovary 2.5–3.5 mm. long; style hirsutulous (rarely almost or quite glabrous), curved at the base, 4–6 mm. long when mature. Drupe translucent pink to red; endocarp turbinate, ridged, 4–6 (mostly 5) mm. long, 3–6-celled but mostly 4-celled.

TYPE: Raivavae, Matotea, alt. 78 m., April 28, 1922, *Stokes 90*, in the Bishop Museum Herbarium.

This species, known from a single island, is closely related to *M. rapense*. Its differences are not very profound but appear to be constant; for instance, no leaves of *M. Stokesii* have been found to show the serrations of *M. rapense*. *M. Stokesii* is evidently more distant from the probable ancestor, *M. laetum*, and it seems likely that the ancestral form which populated the Austral Islands and Rapa was very close to *M. rapense* var. *rapense*.

This species is much more variable than *M. rapense*, and some of its forms diverge widely from the norm. *Fosberg 11737* is remarkable for the petalloid appendages which are present on the stamens, but as no other specimen from the island shows this, the plant had better be regarded as a minor variant.

The inconstancy of style pubescence in *M. Stokesii* raises difficulties in separating it from *M. sandwicense;* the forms of *M. Stokesii* with glabrous styles can be positively distinguished from ssp. *Wilderi* only by their narrower leaf shape. The approach of these forms to ssp. *Wilderi* illustrates the difficulty of defining specific lines in the insular myoporums. Even though the distinctions between the Hawaiian and Austral Island species may thus break down, however, the species are in the main distinct, and it would be unwise to combine them before all the insular myoporums have been carefully studied.

Specimens examined

RAIVAVAE:

Form 1. Style copiously hirsutulous.

Near mountain top, alt. 1,000 ft., *Chapin 871* (NY); Pic Rouge, northwest side, alt. 120 m., *St. John & Fosberg 15947* (BISH); same locality, alt. 150 m., *St. John & Fosberg 15956, 15964* (BISH); Maunanui, ridge, alt. 900 ft., *Stokes 11* (BISH); Matotea, alt. 78 m., *Stokes 90* (BISH, type— as to sheet from Raivavae); "Raivavae," *Whitney expedition 237* (NY).

Form 2. Style hirsutulous; stamens with petalloid appendages.

Vaiuru, N. E. slope, alt. 30 m., *Fosberg 11737* (BISH).

Form 3. Style sparsely hirsutulous to glabrous.

South side of Mt. Turivao, rock ledge, alt. 240 m., *Fosberg 11784* (BISH); south side of Mt. Araua, alt. 300 m., *St. John 16201* (BISH);

Pic Rouge, northwest side, alt. 140 m., *St. John & Fosberg 15957* (BISH); Mt. Taraia, south side, alt. 250 m., *St. John & Kondo 15996* (BISH).

11. **Myoporum rapense** F. Brown, Bishop Mus. Bul. 130: 278–279, fig. 42. 1935.

Shrubs or trees, 1–10 m. high. Leaves lanceolate or somewhat obovate, sharply serrate, glabrous, 4–11.5 cm. long, 0.7–2 cm. broad, acute to acuminate, alate-petiolate. Flowers 1–4 (rarely 5) per axil, often 1 or more abortive; pedicels 0.5–1.5 cm. long. Calyx lobes 5, glandular-dotted, lanceolate and acuminate, 2–3.5 mm. long; margins entire, minutely serrulate, or prominently ciliate. Corolla 5-lobed (rarely 6-lobed), white, pink, or purple-spotted in the throat, with a heavy sweet or sometimes fetid odor, 8–12 mm. long, pubescent within. Stamens 4, all well developed or one a rudiment. Ovary 2.5–3.5 mm. long; style hirsutulous, curved at the base, 4–6 mm. long. Drupe brick- or purplish-red; endocarp turbinate or oblong-ellipsoid, not or scarcely ridged, 5–8 mm. long, 3.5–5.5 mm. wide, 3–6-celled (often one or more cells empty).

This species occurs on Tubuai, Raivavae, and Rapa and is more constant morphologically than is its probable derivative *M. Stokesii*. It is separated from this latter species by characters which are very stable for the genus *Myoporum*, and only one specimen is in any way intermediate. The form of *M. rapense* on Raivavae has typical leaves and fruit but flowers more nearly the size of *M. Stokesii*. This form does not seriously break down the boundaries between the two species, however, and it seems best to maintain them as distinct.

While *M. rapense* is clearly separable from *M. Stokesii*, it is not nearly so easily distinguished from the New Zealand *M. laetum*. For the present, however, its more inconspicuously punctate leaves (fully discussed under Morphological Criteria earlier in this paper) may serve to separate it.

12. **Myoporum rapense** var. **rapense**

Pls. I, 15; II, 25, 37; III, 46

Myoporum rapense F. Brown, Bishop Mus. Bul. 130: 278–279, fig. 42. 1935.

Leaves lanceolate or obovate-lanceolate, 4–10 cm. long, 0.7–2 cm. broad. Calyx lobes lanceolate, acuminate, 2–3 mm. long; margins entire or minutely serrulate. Corolla 8–9 (rarely 11–12) mm. long. Ovary 2.5–3 mm. long; style 4–5 (rarely 6) mm. long. Endocarp 5–8 mm. long, 3.5–5.5 mm. broad, 3–6-celled.

TYPE: Rapa, alt. 170 m., Sept. 13, 1921, *Stokes 161*, in the Bishop Museum Herbarium. Brown (1935:279) cited two collections from Rapa as types. I have chosen the first one as the lectotype, since the number of the other (*Stokes 90*) is the same as the type of *M. Stokesii*.

Specimens examined

RAIVAVAE:

This form has a corolla about 12 mm. long, style 6 mm. long.

Vaiuru, 1 km. east, top of beach, alt. 0.5 m., *Fosberg 11723* (BISH).

RAPA:

This form has a corolla 8–9 mm. long, style 4–5 mm. long.

Anarua, alt. 50 ft., *Stokes 161* (BISH, type); Anarua Valley, southeast ridge of Mt. Perahu, alt. 300 m., *Fosberg 11521* (BISH); Matauri Point, near lower edge of forest, alt. 3 m., *Fosberg 11525* (BISH); Anarua Bay, top of beach, alt. 1 m., *St. John 15707* (BISH); Area, alt. 145 m., *St. John & Fosberg 15280* (BISH); Toutore, west of Mt. Vaitau, alt. 240 m., *St. John & Maireau 15409* (BISH); northeast ridge of Mangaoa Peak, alt. 320 m., *St. John & Maireau 15381* (BISH); north slope of Mt. Lekie, mixed woods, alt. 250 m., *St. John & Maireau 15624* (BISH); Karapo Rahi I. [islet off Rapa], alt. 75 m., *St. John & Maireau 15600* (BISH); Taunoa Ridge, alt. 400 ft., *Stokes 90* (as to sheet from Rapa) (BISH); Hiri, north ridge from Lekie, alt. 500 ft.,

Stokes 217 (BISH, NY); Kulukulu, Hiri, ridge, alt. 170 ft., *Stokes 304* (BISH).

13. **Myoporum rapense** var. **Skottsbergii** Webster, var. nov.

Pls. I, 14; II, 26

Lobae calicis ciliatae.

Leaves elliptic-lanceolate, 5.5–8 cm. long, 1.2–1.7 cm. broad. Calyx lobes ovate, acuminate-tipped, sparsely long-ciliate on the margins, about 2 mm. long. Corolla 10.5–11 mm. long. Ovary 2.5 mm. long; style 4–4.5 mm. long. Color of flowers and fruits unknown; endocarp 5.5–6 mm. long, with 2 fertile and 2 sterile cells in the one fruit cut open.

TYPE: "Toubouia" [=Tubuai], *Cuming 1430*, in the Kew Herbarium.

This variety is known only from the type collection made by Cuming in 1828. One might explain its not having been collected there again by assuming that the locality given on the label is incorrect, but St. John (1940: 88) has studied Cuming's voyages and cites his collection numbers *1423–1433* as being made on Tubuai. A more likely explanation is that the variety is extinct, inasmuch as St. John and Fosberg did not find it in 1934 after a careful search of the few remaining acres of native forest (personal communication from Dr. St. John).

This variety is named in honor of Dr. Carl Skottsberg, who for many years has been a student of *Myoporum* (and numerous other genera) in the Pacific islands.

DOUBTFUL AND EXCLUDED SPECIES

Myoporum ? euphrasioides Hook. & Arn., Bot. Beechey Voy. 67, 1832.

This plant, described from Whitsunday Island (=Pinaki I., Tuamotus), is now known as *Nesogenes euphrasioides* (Hook. & Arn.) A. DC. Because Hooker and Arnott included the Tuamotus in the Society Islands, a number of writers listed *Myoporum euphrasioides* from the latter group.

Myoporum rimatarense F. Brown, Bishop Mus. Bul. 130: 280, fig. 43. 1935.

This species from Rimatara, Austral Islands, is known from such fragmentary material (the flowers being unknown) that its exact disposition is impossible. Judging from the leaf shape it might be a form of *M. sandwicense* ssp. *Wilderi*, but this is only a guess. St. John tells me that the vegetation on Rimatara is badly despoiled and that the *Myoporum* there may well be extinct.

Myoporum tenuifolium Forst f., Prodr. 44. 1786.

Nadeaud (1897: 113) credits this species to Tahiti (as a cultivated plant) and to Raivavae. The Raivavae plant is probably *M. Stokesii*. The cultivated Tahitian plant may also be *M. Stokesii*, but I have seen no specimens. *M. tenuifolium* is one of the most widespread species of the genus, occurring from New Caledonia into Micronesia, but it has not been collected in Polynesia proper.

REFERENCES

BENNETT, GEORGE. 1832. An account of the sandal wood tree (*Santalum*), with observations on some of the botanical productions of the Sandwich Islands. *Mag. Nat. Hist.* 5: 255–261.

BENTHAM, GEORGE. 1870. *Flora Australiensis.* Vol. 5. viii+599 pp. L. Reeve & Co., London.

BRIGHAM, WILLIAM T. 1908. *The ancient Hawaiian house.* Bernice P. Bishop Mus., Mem. 2(3): iv+185–378, pls. 18–40, 178 figs.

BROWN, FOREST B. H. 1935. *Flora of Southeastern Polynesia—III. Dicotyledons.* Bernice P. Bishop Mus., Bul. 130: ii+386 pp., 9 pls., 70 figs.

CHEESEMAN, T. F. 1903. The flora of Rarotonga, the chief island of the Cook Group. *Linn. Soc. Lond., Trans. Bot.* II, 6(6): 261–313, map, pls. 31–35.

DE CANDOLLE, ALPHONSE. 1847. *Prodromus systematis naturalis regni vegetabilis*. Vol. 11: 1–736. Victoris Masson, Paris.

DEGENER, OTTO. 1930. *Illustrated guide to the more common or noteworthy ferns and flowering plants of Hawaii National Park with descriptions of ancient Hawaiian customs and an introduction to the geologic history of the islands*. xv+312 pp., frontisp., 95 pls., 45 figs. Honolulu Star-Bulletin, Ltd., Honolulu.

EGLER, FRANK E. 1947. Arid southeast Oahu vegetation, Hawaii. *Ecol. Monog.* 17: 383–435, 41 figs.

FORBES, CHARLES N. 1913. Notes on the flora of Kahoolawe and Molokini. *Bernice P. Bishop Mus., Occas. Papers* 5(3): 85–97, 7 figs.

FORSTER, G. (=J. G. A.). 1786. *Florulae insularum australium prodromus*. 103 pp. Dietrich, Gottingen.

FOSBERG, F. RAYMOND. 1943. *The Polynesian species of* Hedyotis (*Rubiaceae*). Bernice P. Bishop Mus., Bul. 174: 1–102, 4 pls., 9 figs.

GRAY, ASA. 1866. Characters of some new or obscure species of plants, of monopetalous orders, in the collection of the United States South Pacific Exploring Expedition under Captain Charles Wilkes, U.S.N. *Amer. Acad. Arts and Sci., Proc.* 6: 37–55.

HOOKER, WILLIAM JACKSON, and G. A. ARNOTT. 1830–1841. *The botany of Captain Beechey's voyage comprising an account of the plants collected by Messrs. Lay and Collie, and other officers of the expedition during the voyage to the Pacific and Bering's Straits, performed in His Majesty's ship*, Blossom, *under the command of Captain F. W. Beechey . . . in the years 1825, 26, 27, and 28*. ii+485 pp., 99 pls. Treuttel, Wurz, Treuttel Jr., & Richter, London.

KRAENZLIN, F. 1929. Beitrage zur Kenntnis der familie der Myoporinae R. Br. *Fedde Repert. Sp. Nov. Beih.* 54: 1–129.

LÉVÉILLE, H. 1912. Decades plantarum novarum XC–XCII. *Fedde Repert. Sp. Nov.* 11: 63–67.

NADEAUD, J. 1897. Note sur quelques plantes rares ou peu connues de Tahiti. *Jour. Bot. Morot* 11(7): 113–120.

ROCK, JOSEPH F. 1913. *The indigenous trees of the Hawaiian Islands*. iv+518 pp., 215 pls. Honolulu.

ST. JOHN, HAROLD. 1940. Itinerary of Hugh Cuming in Polynesia. *Bernice P. Bishop Mus., Occas. Papers* 26(4): 81–90, portr.

SKOTTSBERG, CARL. 1933. *Myoporum* in Rarotonga. *Acta Horti Gotob.* 8: 147–167, 48 figs.

SOLEREDER, HANS. 1899. *Systematische Anatomie der Dicotyledonen*. xii+984 pp., 189 figs. Ferdinand Enke, Stuttgart.

WETTSTEIN, R. VON. 1895. Myoporaceae. In: Engler & Prantl, *Naturl. Pflanzenfam.* IV: 3b., 354–360, figs. 142–144. Wilhelm Engelmann, Leipzig.

WILDER, GERRIT PARMILE. 1931. *Flora of of Rarotonga*. Bernice P. Bishop Mus., Bul. 86: 1–113, 8 pls., 3 figs.

ZIMMERMAN, ELWOOD C. 1948. *Insects of Hawaii*. Vol. I: Introduction. xx+206 pp., 52 figs. University of Hawaii Press, Honolulu.

Record of the Shark *Carcharhinus longimanus*, Accompanied by *Naucrates* and *Remora*, from the East-Central Pacific[1]

CARL L. HUBBS[2]

IN THEIR MASTERLY TREATISE on the sharks of the western North Atlantic, Bigelow and Schroeder (1948: 354–364, figs. 64–65), in untangling some complicated synonymies, showed that the pelagic species commonly known as *Carcharhinus lamia* (Risso) cannot bear this name, but should be called *C. longimanus* (Poey). The literature is in such confusion that they were unable to verify the occurrence of this species in any ocean other than the Atlantic. It is therefore gratifying to obtain evidence promptly that it also inhabits the eastern tropical Pacific. This evidence is provided in the form of a photograph of an adult female specimen caught at Lat. 08° 16′ N., Long. 125° 43′ W., by A. J. Carsola and Jeremiah F. Black of the United States Navy Electronics Laboratory, on the ship "Serrano."[3] This picture (Fig. 1) corresponds very closely with Bigelow and Schroeder's figure of an adult female, especially in the highly diagnostic features of the broadly rounded first dorsal fin, the markedly enlarged and round-tipped pectoral fin, the convex posterior border of the lower caudal lobe, the size and position of the anal and second dorsal fins, the extremely short snout in front of the nostrils, and the coloration. There can be virtually no doubt as to the identification.

The lack of previous records from the eastern Pacific (see Beebe and Tee-Van, 1941, and Fowler, 1944) is explicable, for nearly all previous collecting has been near shore, and Bigelow and Schroeder indicate that this species is more strictly pelagic than any other in the Atlantic and is more definitely tropical than most of them. The new Pacific record station lies far off Mexico and east-southeast of the Hawaiian Islands.

The circumstances of the capture of the Pacific specimen are given in the log of the "Serrano," as follows:

27 May 1949, 1516 PST. A gray shark with white fin and tail tips was observed swimming around the ship about this time; three fish, each about one foot long and decorated by transverse black and silver stripes maintained formation with the shark, one being about a foot in front of him, another just below his body mid-section and another just above him. The shark was baited with a light hook and line, shot, and pulled onto deck (see picture).

The banded fish were of course *Naucrates ductor* (Linnaeus). Like the *Carcharhinus* that they were accompanying, the pilotfish are referable to a circumtropical species. It is true that Fowler (1905: 62–65, fig. 3) described the Pacific form as a distinct species, *Naucrates polysarcus*, partly on the basis of differences pointed out by Gill (1862: 440–441), but it now seems likely that the distinction was based on juvenile characters. The supposedly deeper body and the longer fins may well be characters of the young. Meek and Hildebrand (1925: 401) stated that "the

[1]Contributions from the Scripps Institution of Oceanography, New Series, No. 493. Manuscript received February 1, 1950.

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[3]Thanks are due E. R. Anderson of the United States Navy Electronics Laboratory for the transmission of data, photograph, and specimen.

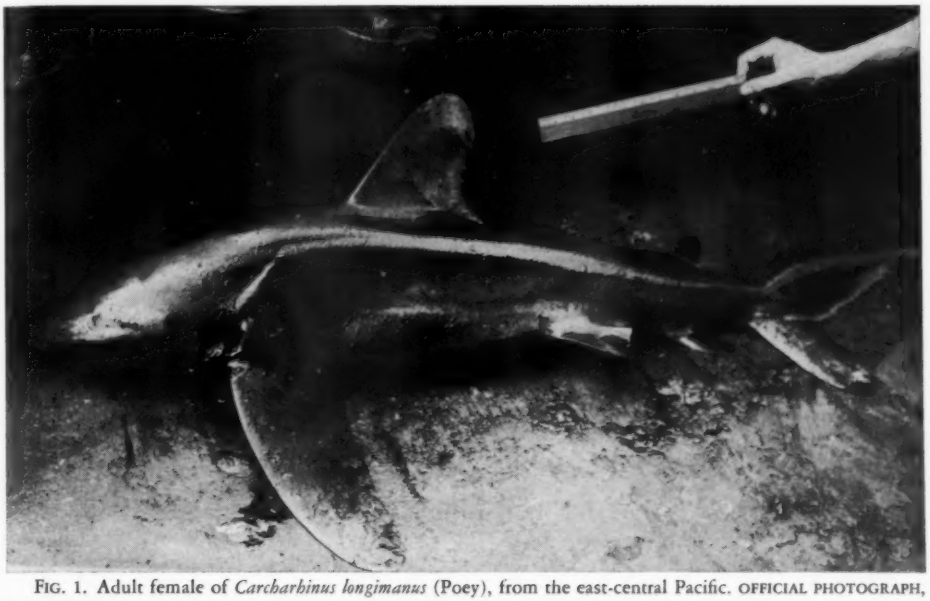

FIG. 1. Adult female of *Carcharhinus longimanus* (Poey), from the east-central Pacific. OFFICIAL PHOTOGRAPH, U. S. NAVY.

young appear to be deeper and more strongly compressed than the adult"; Wakiya (1924: 232, pl. 38, fig. 2), however, indicated that the young of "*Naucrates indicus*" are more slender than the adult. The original figure of *N. polysarcus* suggests that the extreme depth ascribed to the type may be attributed to its poor preservation. The different scale count, also emphasized by Fowler, is probably not significant, for the scales are too irregularly arranged to be counted precisely. Jordan and Starks (1907: 72) found that the supposed characters do not hold for a Pacific species, and Meek and Hildebrand, though failing to include *polysarcus* in their synonymy, refer Pacific material to *N. ductor*. Walford (1937: 66–68) likewise referred the Pacific form to *N. ductor* (and by mistake labeled the figure, which was taken from Jordan and Evermann, as "from Jordan and McGregor, 1898"). An adult specimen 325 mm. in standard length, recently received from off the Pacific coast of Mexico, has the slender form and the short fins ascribed by Fowler to the Atlantic form. Recently, Fowler (1944: 423, 500) treated *polysarcus* as a subspecies of *ductor*.

From the shark there was taken a specimen, 105 mm. long, of another circumtropical species, *Remora remora* (Linnaeus). It agrees satisfactorily with material from southern California.

The specific integrity of such circumtropical pelagic fishes poses a problem in speciation, since widespread littoral types of the tropics, as well as most pantemperate types, in contrast, are ordinarily differentiated into allopatric subspecies or species, though their period of isolation has ordinarily been no longer, often briefer, than that of the land-separated populations of the tropical pelagic forms. The explanation seems to lie both in the uniformity of the tropical pelagic environment and in the relationship between the population structure and the rate of speciation. Large, widespread populations that are not disrupted into effective reproductive units

are now generally held, on the basis of Wright's analyses (1940*a*, *b;* 1942), to be little subject to differentiation.

ADDENDUM

After this manuscript was submitted for publication, Springer (1950: 2, 7–8) erected a distinct genus, *Pterolamia*, for the reception of *Carcharhinus longimanus* and, probably also, of *C. insularum* (Snyder), a species described from the Hawaiian Islands. He separated this nominal genus from *Eulamia* solely on the basis of the rounded tips of the dorsal and pectoral fins. Since the sharpness of these fins varies considerably and since the rounded tips seem to involve merely the retention of an embryonic feature, I am disinclined to accept the generic separation. Some other species of *Carcharhinus*, for example, *C. falciformis* (Müller and Henle) as described by Bigelow and Schroeder (1948: 329–333, figs. 56–57), have the pectoral scarcely more pointed than in *C. longimanus* and have the dorsal distinctly though less broadly rounded. Nor does Springer's separation of *Eulamia* from *Carcharhinus* seem justified on the basis of the presence or absence of a middorsal ridge—a very tenuous distinction that depends in large part on the condition of preservation and that seems to be inconsistent, in some species at least.

That *Carcharhinus longimanus* may be common in the open equatorial Pacific is suggested by a picture in the recently published book *Kon-Tiki*, showing nine sharks caught in one day (Heyerdahl, 1950: lower figure of 2d pl. following p. 176; accompanying text apparently on pp. 205–206). So far as is obvious all sharks in this picture seem referable to the pelagic species under discussion. This identification is ventured on the basis of the showing of certain diagnostic characters, in particular the broadly rounded pectoral fins, much longer than the head; the far-forward position of the nostrils on the very short, strongly rounded, laterally angulated snout; and the plain coloration. The location of the catch is not specified, but the context indicates that it was in the South Equatorial Current somewhere between Perú and the Tuamotu Archipelago.

REFERENCES

BEEBE, WILLIAM, and JOHN TEE-VAN. 1941. Eastern Pacific expeditions of the New York Zoological Society. XXV. Fishes from the tropical eastern Pacific. [From Cedros Island, Lower California, south to the Galápagos Islands and northern Peru.] Part 2. Sharks. *Zoologica* 26: 93–122, figs. 1–34, pls. 1–2.

BIGELOW, HENRY B., and WILLIAM C. SCHROEDER. 1948. Fishes of the western North Atlantic. Sharks. *Sears Found. Mar. Res., Mem.* 1, Pt. 1, Chap. 3: 59–576, figs. 6–106.

FOWLER, HENRY W. 1905. New, rare or little-known scombroids. No. II. *Acad. Nat. Sci. Phila., Proc.* 57: 56–88, figs. 1–5.

——— 1944. Results of the Fifth George Vanderbilt Expedition (1941) (Bahamas, Caribbean Sea, Panama, Galápagos Archipelago and Mexican Pacific islands). The fishes. *Acad. Nat. Sci. Phila., Monogr.* 6: 57–529, figs. 1–268, pls. 1–20.

GILL, THEODORE. 1862. Synopsis of the carangoids of the eastern coast of North America. *Acad. Nat. Sci. Phila., Proc.* 1862: 430–443.

HEYERDAHL, THOR. 1950. *Kon-Tiki. Across the Pacific by raft.* 304 pp., 40 pls. Rand McNally & Co., Chicago.

JORDAN, DAVID STARR, and EDWIN CHAPIN STARKS. 1907. Notes on fishes from the island of Santa Catalina, southern California. *U. S. Natl. Mus., Proc.* 32: 67–77, figs. 1–8.

MEEK, SETH E., and SAMUEL F. HILDEBRAND. 1925. The marine fishes of Panama. *Field Mus. Nat. Hist., Publ.* 226 (Zool. Ser., 15): i–xix, 331–707, pls. 25–71.

SPRINGER, STEWART. 1950. A revision of North American sharks allied to the genus *Carcharhinus*. *Amer. Mus. Novitates* 1451: 1–13.

WAKIYA, YOJIRO. 1924. The carangoid fishes of Japan. *Carnegie Mus., Ann.* 15: 139–292, pls. 15–38.

WALFORD, LIONEL A. 1937. *Marine game fishes of the Pacific Coast from Alaska to the Equator*. xxix+205 pp., many figs., pls. 1–69. University of California Press, Berkeley.

WRIGHT, SEWALL. 1940*a*. Breeding structure of populations in relation to speciation. *Amer. Nat.* 74: 232–248, figs. 1–3.

——— 1940*b*. The statistical consequences of heredity in relation to speciation. In: *The New Systematics*, pp. 161–183, figs. 1–7. Oxford University Press, Oxford.

——— 1942. Statistical genetics and evolution. *Amer. Math. Soc., Bul.* 48: 223–246, figs. 1–10.

Common and Aberrant Flowers of *Cassia fistula*

MARIE C. NEAL[1]

WHILE COLLECTING HERBARIUM SPECIMENS from golden shower trees (*Cassia fistula* L., a legume from India) at my home in Nuuanu Valley, Honolulu, I noticed that three of our four trees (A, C, D) bore the common form of flowers and that a fourth (B) bore aberrant forms. This discovery led to the examination of other trees of the same species. After studying from June to September, 1948, four or more flowers of each of 26 trees of *C. fistula* in seven different localities in Honolulu, I found that trees A, C, and D definitely bore the common form of flowers, which were nearly uniform. Only tree B bore flowers deviating distinctly from those borne by the other trees. Examination of all these flowers and also of literature dealing with *C. fistula* led to two conclusions: (1) The stamens of the common form of *C. fistula* needed redescription; and (2) the petals, sepals, and stamens of the aberrant form of *C. fistula* differed in several ways from those of the common form.

COMMON FLOWERS

The common form of the flower of *C. fistula* has 5 petals, 5 sepals, and 10 stamens, and it has been described many times. Wight (1840, pl. 269) has a figure which more or less epitomizes these descriptions and from which is here reproduced a detail (Fig. 1), showing flowers for comparison with my drawing (Fig. 2). In Wight's figure, the three shortest stamens appear to be alike. The petals and sepals of published descriptions seemingly were like those of flowers on 25 of the trees examined by me. The stamens, however, were

FIG. 1. Flowers of *Cassia fistula*, reproduced from Wight's plate; letters added to petals to agree with Figure 2.

different. As seen in a diagram of the receptacle (Fig. 3), the 10 stamens are actually arranged in two series, the five inner ones being opposite the five petals, the five outer ones being opposite the five sepals. The five inner stamens, Nos. 2, 4, 6, 8, 10 (Fig. 2, *A*, *B*; Fig. 4, *A–D*), have rather short filaments and versatile, two-celled, slightly compressed, curving-obovoid anthers, each cell opening by a basal pore. No. 2, the uppermost stamen,

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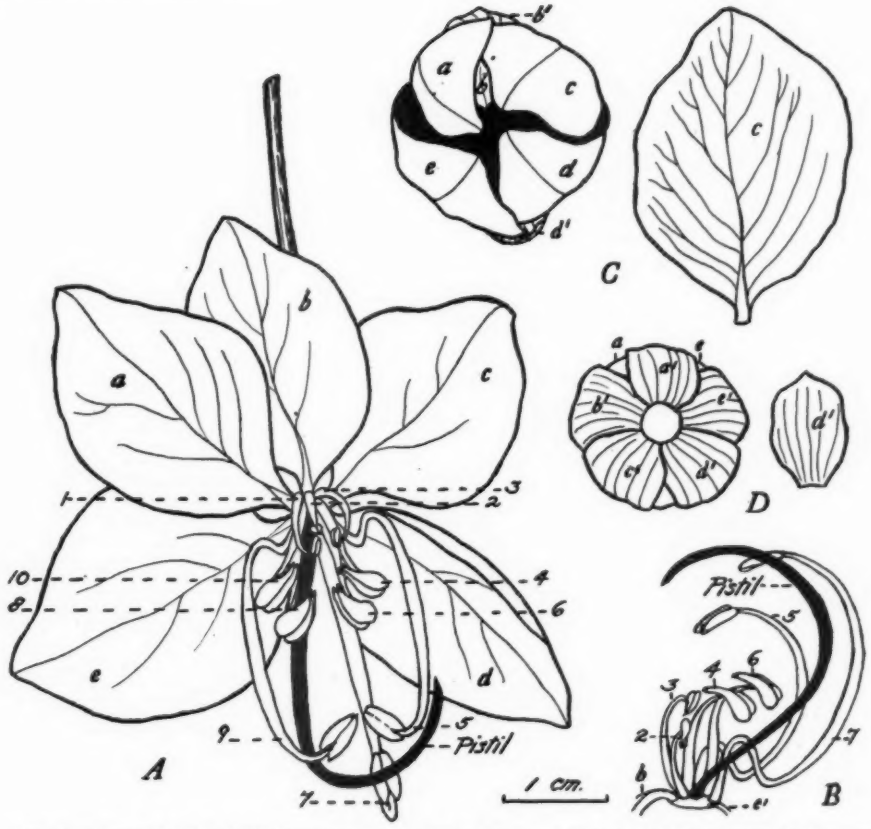

FIG. 2. Flower of *Cassia fistula* from tree C. *A*, Front view: *a–e*, petals; 1, 3, 5, 7, 9, outer, fertile stamens; 2, 4, 6, 8, 10, inner, sterile, starch-bearing stamens. *B*, Arrangement of stamens on right side of flower. *C*, Bud, front view: *a–e*, petals; *c*, single petal. *D*, Bud, back view: *a'–e'*, sepals; *d'*, single sepal.

has the shortest filament and (with Nos. 1 and 3) the smallest anther, and it faces Nos. 4, 6, 8, and 10. Nos. 4 and 10 are paired and are borne on longer filaments than No. 2. Nos. 6 and 8 are paired and are borne on slightly longer filaments than Nos. 4 and 10. All five of these stamens yield pollen.

The five outer stamens, Nos. 1, 3, 5, 7, 9 (Fig. 2, *A*, *B;* Fig. 4, *E–H*), have two-celled, compressed, ovoid anthers, each cell opening by an interrupted longitudinal cleft. Two of these stamens, the upper ones (Nos. 1 and 3), are paired and have short, twisted filaments, little longer than the filament of No. 2, and small, versatile anthers about the size of the anther of No. 2. The other three, lower stamens (Nos. 5, 7, 9), are similar to one another. They have the longest filaments, which curve outward after making a short backward bend at the base, and they bear at their distant tips anthers tending to be slightly smaller than those of Nos. 4, 6, 8, and 10; and though they are not basifixed they are not versatile, but continue in a line with their filaments. All five of these stamens yield pollen.

My description of the 10 stamens does not agree entirely with any I have found in botanical literature. Taubert (1891: 158) states in a summary of subgenera of *Cassia* that sub-

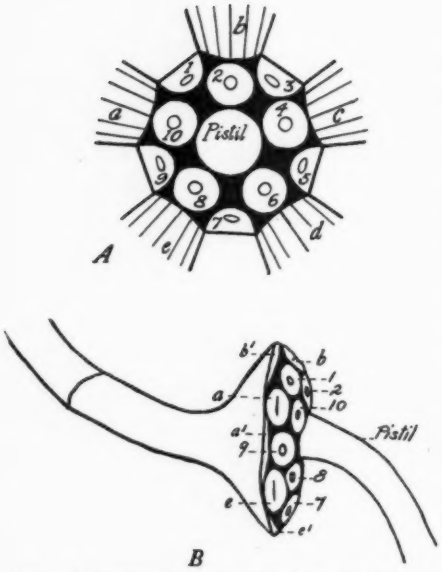

FIG. 3. Receptacle of common form of flower of *Cassia fistula*. *A*, Diagram, front view, showing points of attachment of stamens (1–10) in relation to petals (*a*–*e*) and pistil. *B*, Side view, showing also points of attachment of sepals *a'*, *b'*, *e'*.

genus *Fistula*, to which *C. fistula* belongs, has the three lower stamens (my Nos. 5, 7, 9) with long, bent filaments, and with anthers opening by longitudinal clefts; the seven upper stamens with short filaments and with anthers opening by basal pores; the anthers of the one to three uppermost stamens (my Nos. 1, 2, 3) sometimes abortive. This description of the stamens of *C. fistula* or the subgenus *Fistula* is the description commonly found, the majority of opinions being that the three smallest stamens (my Nos. 1, 2, 3) were alike and without pollen (and, according to some authorities, indehiscent); that the arrangement was seven (or four) anthers with basal pores and the three on long filaments with longitudinal clefts.

Examples of descriptions of the stamens of *C. fistula* follow:—Bentham and Hooker (1865: 572): "Stamina perfecta 10, filamentis 3 inferioribus elongatis, antheris saepius oblongis breviter 2-rimosis, 7 superioribus abbreviatis antheris minute 2-porosis." Trimen (1894: 103, 104): "3 lowest stam. with very long doubly curved exserted fil. and oblong anth. dehiscing longitudinally, 4 lat. ones with short straight fil. and versatile anth. opening by pores at the base, 3 uppermost ones much smaller, erect, with indehiscent abortive anth." Brandis (1907: 253): "The three lower stamens have long curved filaments and anthers, which open by longitudinal slits, four stamens have short filaments and anthers opening by basal pores; the rest have minute anthers without pollen." Rock (1920: 75): "Three stamens with long filaments, 7 stamens with short filaments, anthers of three basifixed opening in longitudinal slits, anthers of seven dorsifixed opening in basilar pores."

As seen by my diagrams and descriptions, the arrangement is of five stamens of each of two kinds in two series, one series opposite the petals, the other opposite the sepals. I have examined the pollen of the "abortive" stamens (Nos. 1, 2, 3) and found apparently normal grains, some slightly smaller than some of those of No. 8, for example, which, however, were turgid with starch. Some of the grains of Nos. 1, 2, 3, also, were slightly smaller than those of Nos. 5, 7, 9, even after the starch contents of Nos. 5, 7, 9 had evidently been converted in mature flowers from starch by diastase (Tischler, 1910: 241). Grains of Nos. 1, 2, 3, from flowers at different stages of development, were tested for starch and dextrin (with iodine dissolved in potassium iodide) and were found to contain varying amounts of both. Thus it seems probable that the small stamens do function—Nos. 1 and 3 like Nos. 5, 7, 9, No. 2 like Nos. 4, 6, 8, 10.

Tischler (1910: 220) agreed with Knuth (1904: 375–377) in Knuth's description of the stamens of *C. fistula*, which is translated as follows (Knuth had studied the flower ecology of *C. fistula* in Buitenzorg):

Cassia fistula has three abortive stamens; these have anthers to 2 mm. long, which are

bent inward and are borne on filaments to 10 mm. long. Because of their nature and position they serve chiefly as footholds for the wood bee. Next to them are the four starch-bearing, sterile stamens with filaments 10 mm. long and anthers 5 mm. long. Three fertile stamens arise from the flower's base, the filament basally being directed upward, then after 5 mm. suddenly turning backward, and finally bending in a large curve out of the flower, so that the 5×2 mm. anthers are to 25 mm. from the flower base.

Tischler states that he has nothing to add to this description and that like Knuth he saw the pollinating wood bee "milk" the starch-bearing anthers (my Nos. 4, 6, 8, 10) for food and get pollinated by the fertile anthers (my Nos. 5, 7, 9), the pollen of which it then carried to stigmas of other flowers.

The position of the style may be between stamens Nos. 5 and 7 or between Nos. 7 and 9.

ABERRANT FLOWERS

The cause of the aberrations in tree B is not known. The four trees in our garden, A, B, C, D, are about 12 years old. The 22 other trees examined are probably older. The general aspect of tree B is like that of the common form of *C. fistula*. But the leaves are slightly shorter and the leaflets smaller than those of A, C, D; none, however, was malformed. According to Ridgway's Color Chart, the "wax yellow" flowers of tree B are a duller yellow than the "lemon chrome" flowers of tree A, for example; this comparison, on being analyzed, shows that the flowers of both B and A have the same hue, orange-yellow-yellow (25 per cent orange, 75 per cent yellow), but that "wax yellow" is grayer, a stage nearer neutral. Besides other differences of the flowers, some racemes though at first as large soon become small and rounded, with flowers clustered at the tip only, instead of remaining long and more or less obconical, as in the common form; other racemes are small and rounded from the beginning. The seeds look like those of tree A, for example; but the pods are far fewer, some are shorter, and others have constrictions.

All these slight differences might well be within the range of the species. Hybridism does not explain the differences, since the regular shaped sepals, petals, and stamens found among the irregular shaped ones of tree B were much like those of the common form of flower of trees A, C, and D.

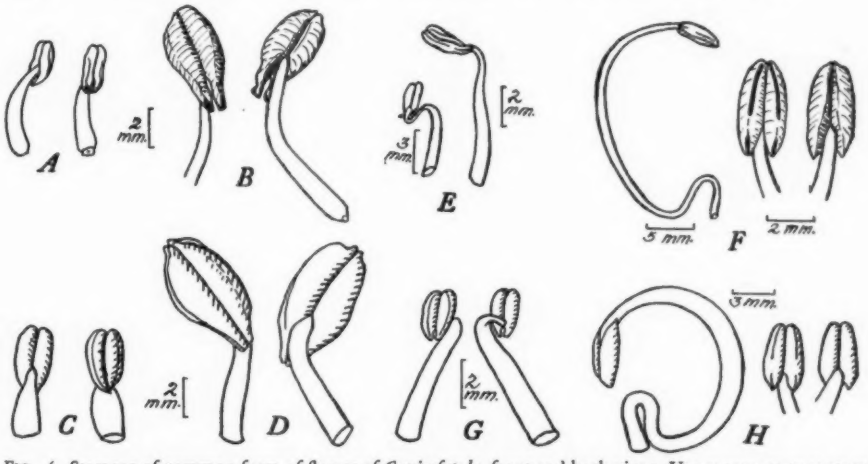

FIG. 4. Stamens of common form of flower of *Cassia fistula*, front and back views. Upper row: mature stamens from open flower, anther cells open. Lower row: stamens from bud, anther cells not open. *A* and *C*, No. 2; *B* and *D*, No. 8; *E* and *G*, No. 1 (*E* shows No. 1 from two different flowers); *F* and *H*, No. 9.

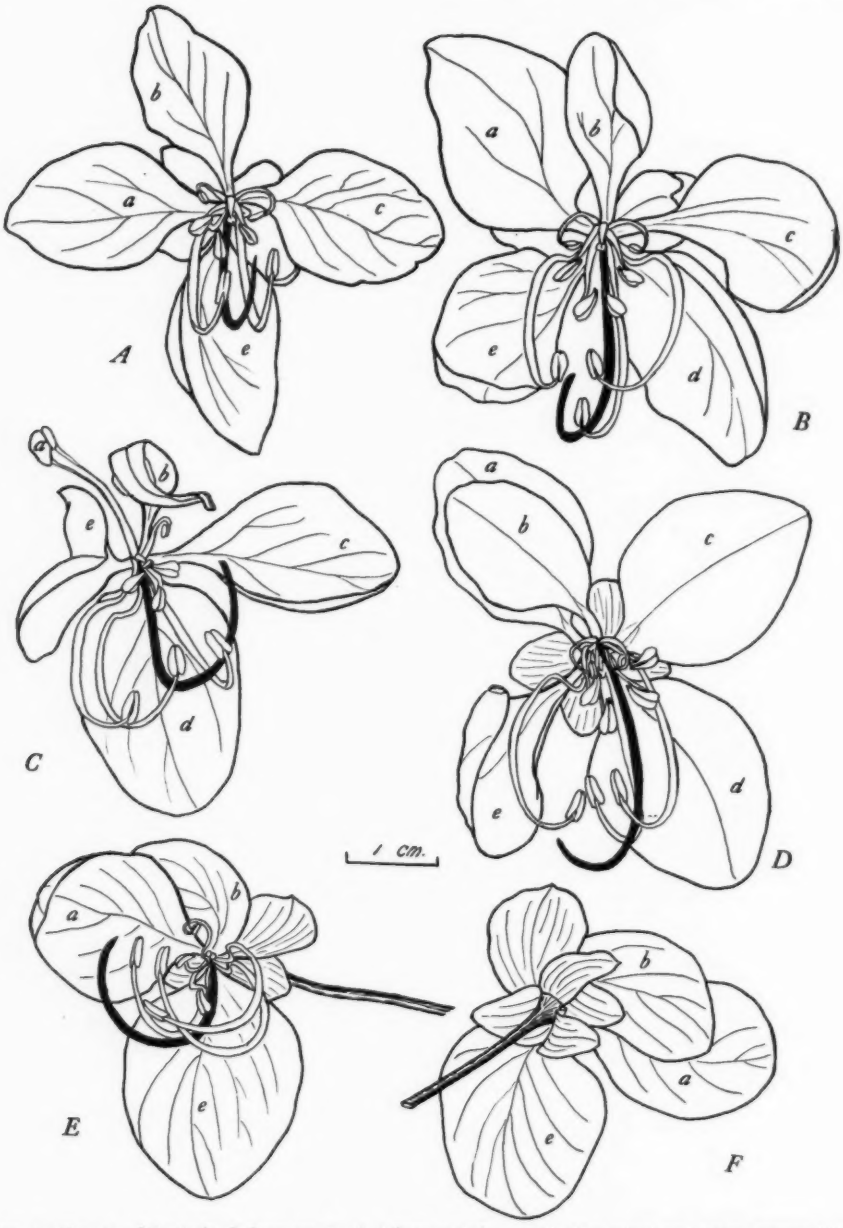

FIG. 5. Flowers of *Cassia fistula* from tree B. *A*, A form with four petals (*d* missing) and eight stamens (Nos. 6, 7 missing). *B*, A slightly irregular form with the common number of stamens, petals, and sepals. *C*, A form with three of five petals much modified; eight stamens (Nos. 1, 8 missing), with anthers borne on two petals (see Fig. 6, *C*). *D*, A form with three of five petals contorted, one bearing an anther cell; nine stamens, No. 2 missing. *E*, A form with three petals (*c* and *d* missing); five sepals; seven stamens (Nos. 3, 4, 6 missing). *F*, Back view of *E*.

The possibility that 2,4–D was the cause has been suggested. For 2 or 3 years before this study was made, trees A and B were exposed to 2,4–D, which was applied in solution from a watering pot on the ground near their trunks in order to rid that part of the lawn of pennywort and other weeds. This treatment did not seem to affect tree A. In July, 1949, a year later, and without another application of 2,4–D, tree B again bore aberrant flower forms. The effect of this hormone-like substance on herbs is temporary and comparatively short (Zimmerman, 1943); but the effect appears later and lasts longer on woody plants. Applications of 2,4–D to weeds along a fence of living hau (*Hibiscus tiliaceus* L.), at Kailua, Oahu, caused malformed leaves on the hau more than 6 months later;[2] flowers, being absent, were not studied. According to Zimmerman (1943), modified organs may well be caused by an environment (or chemicals) which permits different potentialities of the protoplasm to develop, inasmuch as "the so-called 'normal' characters of a plant are but a partial expression of the range of possibilities of which the protoplasm is capable."

Although I had not examined the flowers of tree B in detail until June, 1948, for years before then I had noticed the general appearance of the tree with its small, rounded racemes, and I believe it always has been different. In fact, it may be a sport. If so, this would also explain the comparatively small number of pods, which is characteristic of a sport and is not usually caused by 2,4–D (van Overbeek, 1946). Nonetheless it is possible that fasciation found on tree B in July, 1949, might have been caused by the application of 2,4–D the year before. The tree bore many more flowers in 1949 than in 1948, and among them were found four racemes with conspicuously flattened peduncles and rachises. No fasciation was noticed in 1948.

The striking difference in tree B is in the strange flowers. These vary in the same raceme, and they follow several patterns. One common form of flower on tree B had four petals, four sepals, eight stamens (Fig. 5, *A*). Another form had five petals, three of which were more or less irregular, four or five sepals, and eight to 10 stamens (Fig. 5, *B*, *C*, *D*). A third form had three petals, four or five sepals, and seven or eight stamens (Fig. 5, *E*, *F*).

The pistils were not noticed to differ from those of the common form.

The sepals were not all equal in size and some seemed to function as petals, one being large, rounded, and yellow (instead of green) where a petal was missing (Fig. 5, *E*, *F*). One or both of the innermost sepals (Fig. 2, *D*, *b'*, *e'*) seemed often to be petal-like. Although flowers on some of the 25 other trees examined were often found to have one or both of the inner sepals more or less petal-like, none reached the size of those on tree B.

The petals varied greatly in size and shape, from round to narrow and more or less curved. Some petals combined with filaments or substituted for them and bore anthers.

The stamens were very variable, both as to filaments and anthers. In extreme examples two anthers might combine, those studied combining an odd and even type anther, such as Nos. 3 and 4, with No. 3 at the tip (Fig. 6, *G*). The presence of an anther with either one or two cells on the edge of a petal was common. The anther was always found to be like the anther of stamens Nos. 1, 3, 5, 7, or 9 (Fig. 4, *E–H*), that is, the outer series of stamens opposite the sepals; and its pollen grains contained starch. Nos. 1 and 3 seemed more commonly malformed than 5, 7, or 9. The calloused edge of the petal from its base to the anther suggested a reduced filament. A calloused edge might end bluntly with a vestigial anther or none. A filament might be edged or tipped with yellow petal material. Some of these aberrations are illustrated (Fig. 6, *A–G*). The stamens and petals and the petals and sepals were partly interfunctional. But the stamens and sepals were not. This closer relationship between petals and sta-

[2]Personal communication from A. J. Mangelsdorf, 1949.

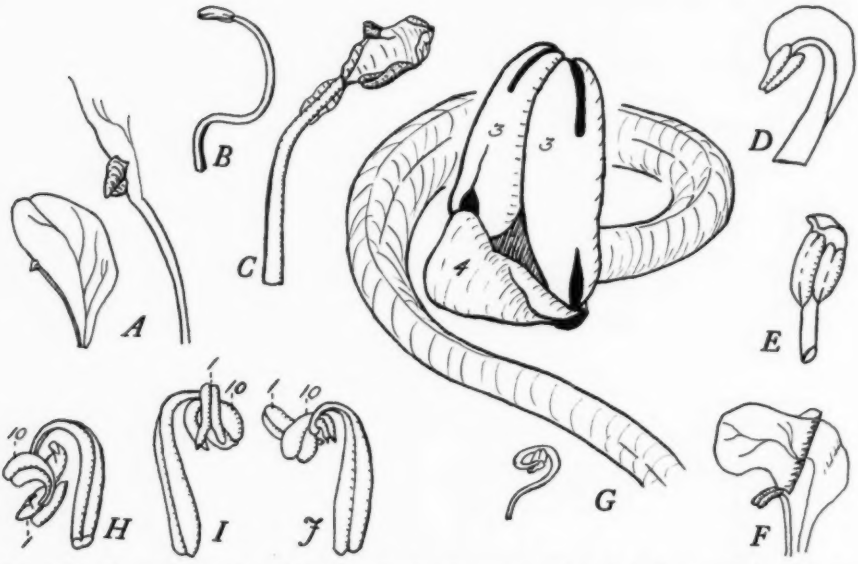

FIG. 6. Peculiar stamens and combinations of reduced stamens and petals in flowers of *Cassia fistula*: tree B (*A–G*), tree H (*H–J*). *A*, Reduced anther in five-petaled flower with eight stamens and four sepals. *B*, Stamen No. 1 imitating missing No. 9 but smaller. *C*, Stamen No. 1 on petal *a* (see Fig. 5, *C*). *D*, Stamen No. 3 on petal *c* (Nos. 7, 8, 9, and petal *b* missing). *E*, Stamen No. 7 on petal *e* (Nos. 1 and 9 missing, one of five petals, *e*, reduced). *F*, Stamen No. 1 on petal *b* (Nos. 9, 10, and petal *e* missing). *G*, Double stamen, Nos. 3 and 4 (Nos. 7, 8, and petal *d* missing). *H, I, J*, Three views of a double stamen, Nos. 1 and 10.

mens is confirmed by observations of plant anatomists, as by Eames (1931: 170), who, in figures of flowers, shows that vascular bundles of sepals, petals, and stamens may be united within the flower but that the bundles of the sepals may branch off much farther down than do those of the petals and stamens. Other instances of stamens being borne on petals or functioning as petals are sometimes found, as in double roses, double hibiscus, peonies, and water lilies. Many flowers having both calyx and corolla, as the mints and verbenas, bear stamens on the corolla tubes. In representatives of the ginger, canna, and maranta families, most of the stamens are sterile, conspicuous, and petal-like.

Among the 26 trees of *C. fistula* examined, two other oddities were found. On two trees, H and I, both near Bishop Museum, two aberrant forms of flowers were found. From tree I, five flowers were taken, four of which were of the common five-parted form. The other had the same arrangement, but six petals, six sepals, and 12 stamens (one extra of each of No. 5 and 6 forms). From tree H, nine flowers were taken. One flower was five-parted but aberrant in having stamens Nos. 4, 10, 6, and 8 not paired but of different lengths, No. 4 being the shortest, No. 10 a little longer, No. 6 longer, and No. 8 longest. Seven flowers were five-parted except that they had only nine stamens, the missing stamen being No. 4 or No. 10. With No. 4 missing, the base of petal *c* came to a point between stamens Nos. 3 and 5, which therefore stood close together. The ninth flower was five-parted throughout, but stamens Nos. 10 and 1 were joined, having a double filament and the anther of No. 1 standing just above the anther of No. 10 (Fig. 6, *H–J*). Some other flowers of tree H were examined and found to be the common five-parted form.

CONCLUSIONS

Conclusions concerning the common form of flower of *C. fistula:* The 10 stamens are arranged in two series. The five inner stamens are opposite the five petals. They have similar filaments and similar basiventral anthers, but one stamen is much smaller than the others. The five outer stamens are opposite the five sepals. They have similar anthers, which open by clefts; but two have smaller anthers and shorter filaments than the other three. The three so-called "abortive" stamens contain and discharge pollen as do the seven larger stamens.

Conclusions concerning the aberrant forms of flowers of *C. fistula* on tree B are that three forms which are irregularly three-, four-, or five-parted seem to dominate. Stamens and petals are more or less interfunctional, as also are sepals and petals, but not stamens and sepals. Inasmuch as all flowers examined on tree B deviated from the common form of the species, this tree may be a sport. It is possible that 2,4-D caused the fasciation in peduncles and rachises found in some inflorescences, but it is not likely that it caused the odd flower forms. It seems improbable that 2,4-D caused reduction in the size of the leaves, which were not malformed. Among the other trees examined, irregular flower forms may develop; but they are rare and not the rule.

REFERENCES

BENTHAM, G., and J. D. HOOKER. 1865. *Genera plantarum.* Vol. 1. xv+1040 pp. Reeve & Co., London.

BRANDIS, DIETRICH. 1907. *Indian trees.* xxxii +767 pp. Archibald Constable & Co., London.

EAMES, A. J. 1931. The vascular anatomy of the flower with refutation of the theory of carpel polymorphism. *Amer. Jour. Bot.* 18: 147–188.

KNUTH, P. 1904. *Handbuch der Blütenbiologie.* Band III. Leipzig.

ROCK, J. F. 1920. *The leguminous plants of Hawaii.* x+234 pp. Experiment Station, Hawaiian Sugar Planters' Association, Honolulu.

TAUBERT, PAUL. 1891. Leguminosae. In: Engler and Prantl, *Die natürlichen Pflanzenfamilien* III, 3. Wilhelm Engelmann, Leipzig.

TISCHLER, G. 1910. Untersuchungen über den Stärkegehalt des Pollens tropischer Gewächse. *Jahrb. f. wiss. Bot.* 47: 220–242.

TRIMEN, HENRY. 1894. *A hand-book of the flora of Ceylon.* Part 2. 392 pp. Dulau & Co., London.

VAN OVERBEEK, J. 1946. Control of flower formation and fruit size in the pineapple. *Bot. Gaz.* 108: 64-73.

WIGHT, ROBERT. 1840. *Icones plantarum indiae orientalis.* Vol. 1. Madras.

ZIMMERMAN, P. W. 1943. The formative influences and comparative effectiveness of various plant hormone-like compounds. *Torreya* 43: 98–115.

A Survey of the Lace-necked Dove in Hawaii

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Streptopelia chinensis chinensis (Scopoli), popularly called the Lace-necked or Spotted Dove because of its characteristic feather pattern, is a common member of the introduced avifauna of the Hawaiian Islands. No information is available concerning the date or exact source of its importation from eastern China to Hawaii, but this dove was very common on Oahu in 1879 (Caum, 1933) and had become established on the other major islands sometime prior to 1900 according to long-time residents interviewed during this survey.

Lace-necked Doves are now permanent residents on all the major Hawaiian Islands. Kahoolawe, a 45-square-mile bombing target under military jurisdiction and 6½ miles offshore from Maui, was not visited during this survey but it is likely that Lace-necked Doves live there. No personal observations were made on Niihau, but the owners of this 72-square-mile island reported in conversation that Lace-necked Doves were well established there and this report has been confirmed by Fisher (MS). The Lace-necked Dove has been observed to fly between the islands of Niihau and Kauai, a distance of 18 miles, and it is conceivable that this species may have voluntarily established itself on the major islands other than Oahu, the probable site of original planting. If this is so, the greatest flight over open water would have occurred between Oahu and Kauai, a distance of 73 miles. The alternative of transportation from one island to another by humans is likewise plausible.

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DISTRIBUTION AND POPULATION

Climatic conditions and the vegetative pattern define the limits of the range of the Lace-necked Dove in the Hawaiian Islands and influence the use of a given area and its population density. The range of this species occurs mostly from sea level to 4,000 feet elevation (Fig. 2), where mean annual temperatures grade from 75° F. at the lowest elevation to 60° F. at the highest elevation; however, in one area on Hawaii it reaches 8,000 feet, where the mean annual temperature is estimated to be around 40° F. Depending on the locality, rainfall in the Hawaiian range of this species varies from less than 10 inches up to a maximum of 250 inches annually. Lace-necked Doves are found in pineapple and sugar cane plantations, in pastures and waste lands, in small truck gardens, homesteads, and urban areas, and in openings of forested sections; dense forests and barren lava are uninhabited.

In order to evaluate this distribution and the abundance of Lace-necked Doves, we have employed the classification of *Vegetation Zones of Hawaii* (Ripperton and Hosaka, 1942), which correlates climatic conditions, the vegetation pattern, and land use throughout Hawaii. While these zones are referred to here, their descriptions and maps are not repeated because of summaries in two other publications (Schwartz and Schwartz, 1949 and 1950).

Range, populations, and densities of the Lace-necked Dove are given according to vegetation zone in Table 1. Strip counts were made in all occupied range and formed the basis for densities representing daytime dis-

TABLE 1

DISTRIBUTION AND POPULATIONS OF THE LACE-NECKED DOVE IN HAWAII BY VEGETATION ZONE

VEGETATION ZONES	SQUARE MILES	SQUARE MILES OCCUPIED	PERCENTAGE OF ZONE OCCUPIED	TOTAL POPULATION	SQUARE MILES WITH DENSITIES OF				
					1–10	11–25	26–50	51–100	101–200
ZONE A									
Hawaii	249	232	94	3,920	82	111	39	0	0
Kauai	23	23	100	1,150	0	0	23	0	0
Lanai	72	72	100	630	66	0	6	0	0
Maui	121	97	80	5,160	3	0	77	17	0
Molokai	64	64	100	5,060	0	24	0	33	7
Oahu	67	51*	76	1,020	0	51	0	0	0
Total	596	539	90	16,940	151	186	145	50	7
ZONE B									
Hawaii	408	397	97	11,090	169	63	165	0	0
Kauai	116	113	97	3,850	0	60	53	0	0
Lanai	57	57	100	2,440	23	0	13	21	0
Maui	138	78	56	4,250	0	0	65	13	0
Molokai	74	74	100	4,200	0	32	12	25	5
Oahu	169	137†	82	3,840	0	117	0	20	0
Total	962	856	89	29,670	192	272	308	79	5
ZONE C_1									
Hawaii	194	183	94	2,940	96	79	8	0	0
Kauai	88	78	89	3,200	8	13	57	0	0
Lanai	10	9	90	400	4	0	2	3	0
Maui	54	37	68	1,710	0	5	32	0	0
Molokai	46	44	96	4,330	0	9	0	28	7
Oahu	146	132	90	3,550	0	106	13	13	0
Total	538	483	90	16,130	108	212	112	44	7
ZONE C_2									
Hawaii	316	196	62	5,740	70	42	84	0	0
Kauai	11	10	91	190	1	9	0	0	0
Lanai	0	0	0	0	0	0	0	0	0
Maui	61	34	56	2,550	0	0	0	34	0
Molokai	0	0	0	0	0	0	0	0	0
Oahu	0	0	0	0	0	0	0	0	0
Total	388	240	62	8,480	71	51	84	34	0
ZONE D_1									
Hawaii	464	417	90	4,880	346	71	0	0	0
Kauai	113	73	65	1,950	2	54	17	0	0
Lanai	2	0	0	0	0	0	0	0	0
Maui	97	69	71	2,810	16	0	53	0	0
Molokai	32	2	6	400	0	0	0	0	2
Oahu	110	101	92	3,440	0	54	29	18	0
Total	818	662	81	13,480	364	179	99	18	2
ZONE D_2									
Hawaii	790	104	13	1,040	104	0	0	0	0
Kauai	194	0	0	0	0	0	0	0	0
Lanai	0	0	0	0	0	0	0	0	0
Maui	151	5	3	250	0	0	5	0	0
Molokai	44	0	0	0	0	0	0	0	0
Oahu	112	30	27	600	0	30	0	0	0
Total	1,291	139	11	1,890	104	30	5	0	0

*Sixteen square miles of urban area occupied by Lace-necked Doves not censused.
†Thirty-two square miles of urban area occupied by Lace-necked Doves not censused.

TABLE 1 (Continued)
DISTRIBUTION AND POPULATIONS OF THE LACE-NECKED DOVE IN HAWAII BY VEGETATION ZONE

VEGETATION ZONES	SQUARE MILES	SQUARE MILES OCCUPIED	PERCENTAGE OF ZONE OCCUPIED	TOTAL POPULATION	SQUARE MILES WITH DENSITIES OF				
					1–10	11–25	26–50	51–100	101–200
ZONE D_3									
Hawaii	353	74	21	740	74	0	0	0	0
Kauai	10	9	90	130	4	5	0	0	0
Lanai	0	0	0	0	0	0	0	0	0
Maui	23	0	0	0	0	0	0	0	0
Molokai	0	0	0	0	0	0	0	0	0
Oahu	0	0	0	0	0	0	0	0	0
Total	386	83	21	870	78	5	0	0	0
ZONE E_1									
Hawaii	647	92	14	940	90	2	0	0	0
Kauai	0	0	0	0	0	0	0	0	0
Lanai	0	0	0	0	0	0	0	0	0
Maui	39	0	0	0	0	0	0	0	0
Molokai	0	0	0	0	0	0	0	0	0
Oahu	0	0	0	0	0	0	0	0	0
Total	686	92	13	940	90	2	0	0	0
ZONE E_2									
Hawaii	503	28	5	280	28	0	0	0	0
Kauai	0	0	0	0	0	0	0	0	0
Lanai	0	0	0	0	0	0	0	0	0
Maui	44	0	0	0	0	0	0	0	0
Molokai	0	0	0	0	0	0	0	0	0
Oahu	0	0	0	0	0	0	0	0	0
Total	547	28	5	280	28	0	0	0	0
ZONE E_3	No Lace-necked Doves								
TOTALS									
Hawaii	4,030	1,723	43	31,570	1,059	368	296	0	0
Kauai	555	306	55	10,470	15	141	150	0	0
Lanai	141	138	98	3,470	93	0	21	24	0
Maui	728	320	44	16,730	19	5	232	64	0
Molokai	260	184	71	13,990	0	65	12	86	21
Oahu	604	451	75	12,450	0	358	42	51	0
Total	6,318	3,122	49	88,680	1,186	937	753	225	21

tribution. These were made in conjunction with inventories taken of other game birds and offered us the most suitable means for establishing satisfactory estimates of population densities. It is realized that a daytime population estimate may include some birds feeding but not roosting in a given zone. However, in the overall population estimate, any error due to this fact appears to be of little consequence. Much of the daily movement takes place within a vegetation zone, and where flyways do exist, they are generally found between vegetation zones A, B, and C_1, all of which rank as dove range of equal quality on the basis of strip-count estimates. Field observations on the amount of available dove food and the occurrence of roosting cover correspond to the general ratings of vegetation zones by population estimates.

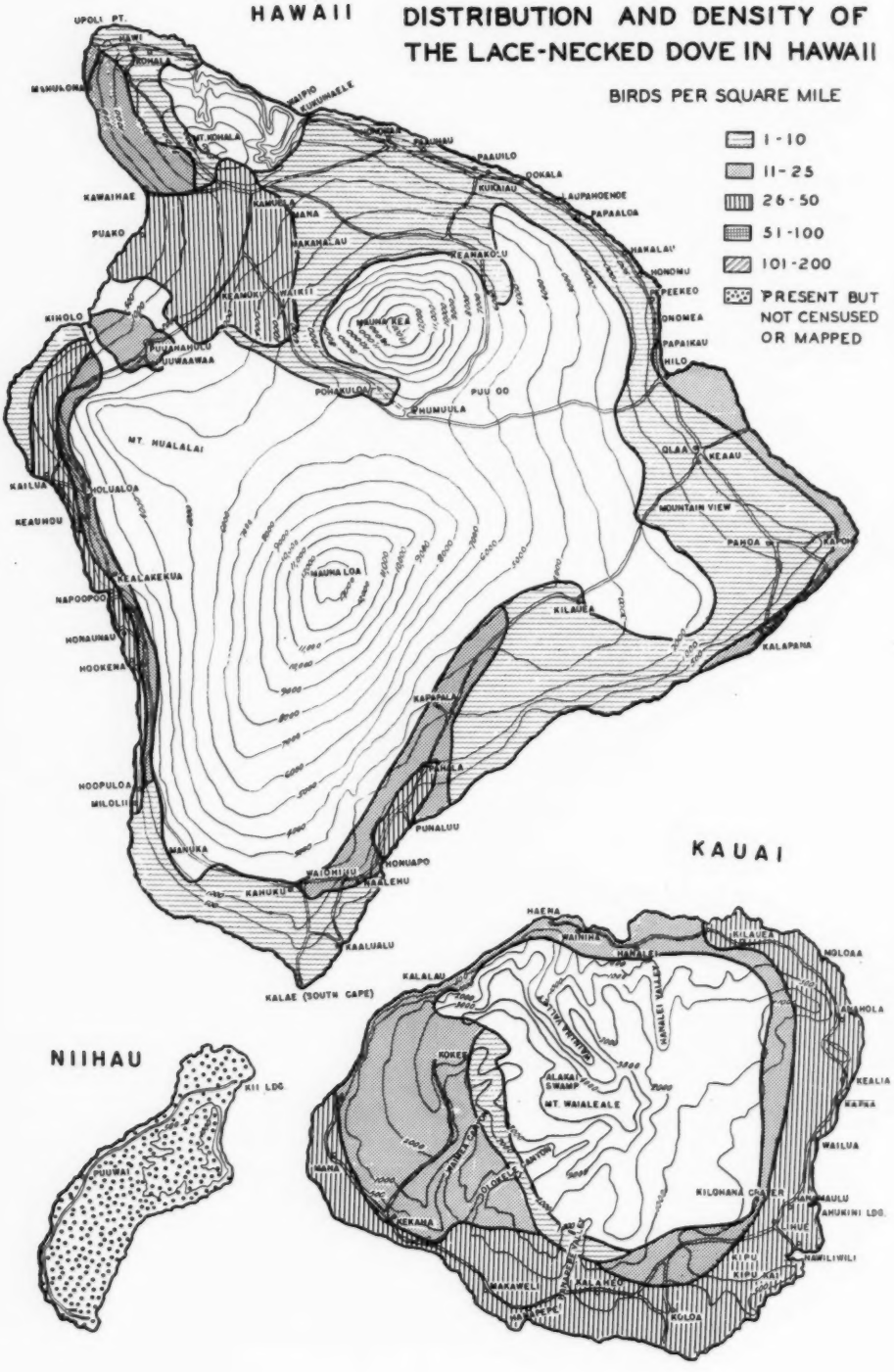
An analysis of Table 1 shows zones A, B, and C_1 to be the best zones for Lace-necked Doves. They all have high percentages of occupancy (89–90 per cent), high populations (16,000–29,000), and include very high

FIG. 1. Adult Lace-necked Dove. Waikii, Hawaii. Elevation 4,700 feet above sea level; April 5, 1946.

densities (up to 200 birds per square mile). These zones occupy the coastal regions below 2,500 feet elevation, where mean temperatures are between 75° and 70° F. annually and where rainfall varies from less than 10 to approximately 60 inches annually. The densest populations in these zones occur on Molokai and are the result of a desirable combination of habitat requirements. One of the most productive areas centers in the region of pineapple cultivation near Hoolehua. A resident population of doves utilizes densely wooded draws and gullies for roosting areas, and forages in old pineapple fields rich in weedy growth and in fallow grain fields and garden plots of adjacent homestead areas. Water is obtained from the fruit of popolo (*Solanum nodiflorum*), scattered livestock watering places, and occasional rain and dew. Two other regions of dove concentration on this island are found in the coastal flats and in areas immediately adjacent. Here, in the excellent roosting sites afforded by algaroba (*Prosopis chilensis*) are numerous stock watering units and some springs. On the adjacent dry open slopes, xerophilous plants such as uhaloa (*Waltheria americana*) and ilima (*Sida* sp.) produce an abundant seed crop utilized by these doves. Between these areas and the Hoolehua area there is considerable exchange of birds, which results in definite flyways.

Zones C_2 and D_1 are classed as intermediate dove range because of an intermediate percentage of occupancy (62–81 per cent), intermediate population (8,000–13,000), and intermediate densities (generally up to 100 birds per square mile). In these zones,

FIG. 2.


HAWAII
DISTRIBUTION AND DENSITY OF THE LACE-NECKED DOVE IN HAWAII
BIRDS PER SQUARE MILE
1-10
11-25
26-50
51-100
101-200
PRESENT BUT NOT CENSUSED OR MAPPED
UPOLI PT.
HAWI
KOHALA
MAHUKONA
MT. KOHALA
KAWAIHAE
PUAKO
KIHOLO
PUUANAHULU
PUUWAAWAA
MAUNA KEA
WAIKII
KEAMOKU
MAKAHALAU
KEANAKOLU
POHAKULOA
PUU OO
PAAUILO
KUKAIAU
PAPAALOA
HAKALAU
HONOMU
PEEKEO
ONOMEA
PAPAIKAU
HILO
PAHOA
KAPOHO
KEAAU
MOUNTAIN VIEW
OLAA
MAUNA LOA
KILAUEA
KALAPANA
MT. HUALALAI
KAILUA
KOLUALOA
KEAUHOU
KEALAKEKUA
NAPOOPOO
HONAUNAU
HOOKENA
KAPAPALA
HOOPULOA
MILOLII
MANUKA
PUNALUU
WAIOHINU
HONUAPO
KAALEHU
KAHUKU
KAALUALU
KALAE (SOUTH CAPE)
KAUAI
HAENA
WAINIHA
HANALEI
KILAUEA
MOLOAA
ANAHOLA
KALALAU
KOKEE
ALAKAI SWAMP
MT. WAIALEALE
KEALIA
KAPAA
WAILUA
KILOHANA CRATER
HANAMAULU
AMUKINI LDG.
LIHUE
KIPU
KIPU KAI
NAWILIWILI
KEKAHA
MANA
MAKAWELI
KALAHEO
KOLOA
NIIHAU
KII LDG.
PUUWAI

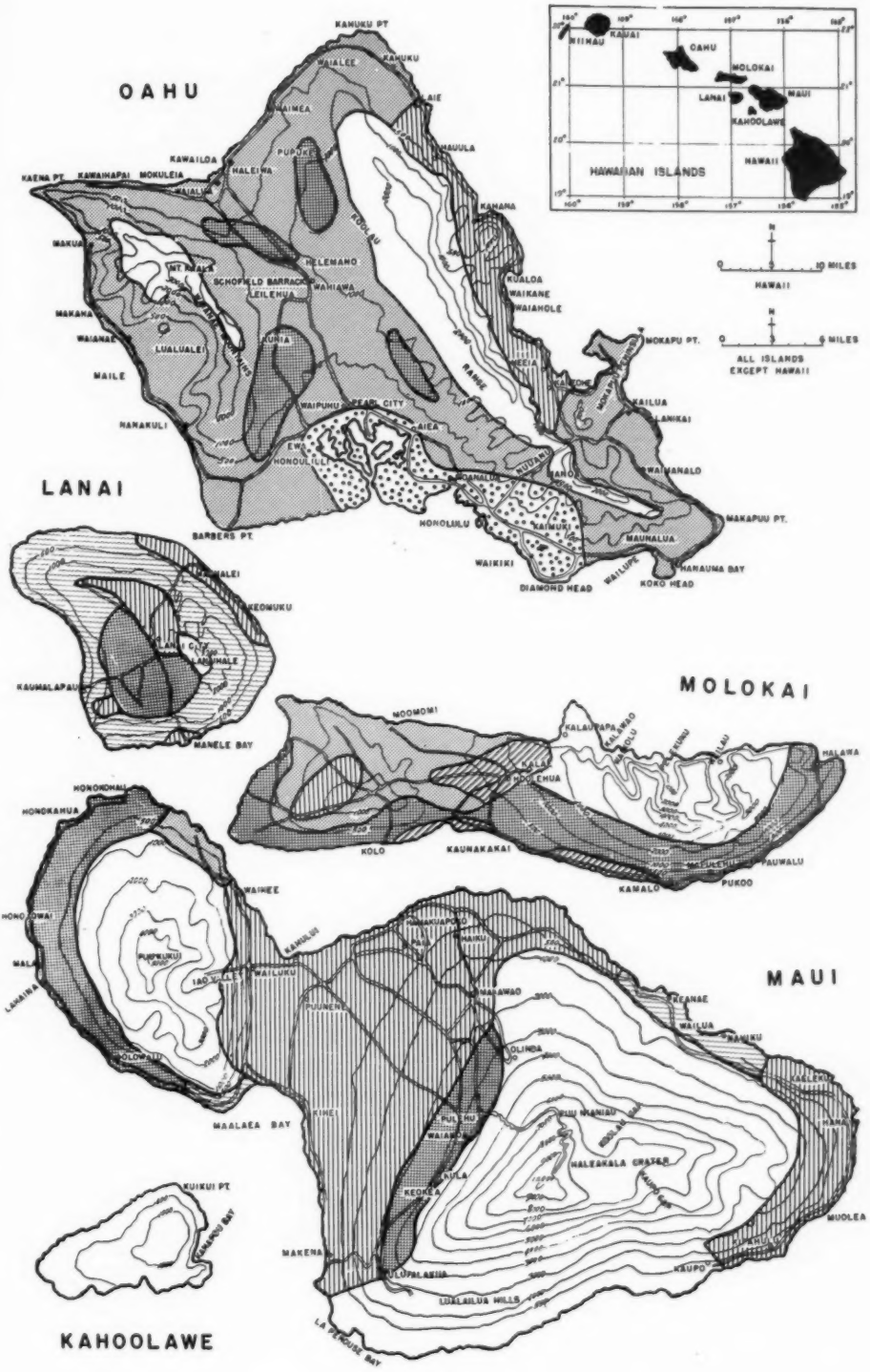

OAHU
KAMUKU PT
WAIALEE
KAHUKU
KAIE
WAIMEA
KAWAILOA
PUPUKEA
HAUULA
HALEIWA
KAENA PT
KAWAIHAPAI
MOKULEIA
WAIALUA
KAHANA
KOOLAU
MAKUA
HELEMANO
MT KAALA
SCHOFIELD BARRACKS
WAHIAWA
LEILEHUA
KUALOA
WAIKANE
WAIAHOLE
MAKAHA
WAIANAE
LUALUALEI
KUNIA
MOKAPU PT
MAILE
MAKUA
KANEOHE
KAILUA
WAIPUNU
PEARL CITY
AIEA
KANEHOA
WAIMANALO
HONOULIULI
HONOLULU
MAKAPUU PT.
BARBERS PT.
KAIMUKI
MAUNALUA
WAIKIKI
WAILUPE
HANAUMA BAY
DIAMOND HEAD
KOKO HEAD
LANAI
KEOMUKU
KAUMALAPAU
LANAI CITY
MANELE BAY
MOLOKAI
NOOMOMI
KALAUPAPA
KALAWAO
KALAE
HOOLEHUA
MALAWA
KOLO
KAUNAKAKAI
KAWALO
PUKOO
PAUWALU
HONOKOHAU
HONOKAHUA
WAIHEE
KAHULUI
HONOLUA
MAUI
WAILUKU
IAO VALLEY
PUUNENE
MAALAEA BAY
KIHEI
KOLOA
MAKENA
KUIKUI PT
LA PERouse BAY
KAHOOLAWE
HAWAIIAN ISLANDS
NIIHAU
KAUAI
OAHU
MOLOKAI
LANAI
MAUI
KAHOOLAWE
HAWAII
HAWAII
0 5 10 MILES
ALL ISLANDS EXCEPT HAWAII
0 3 6 MILES

FIG. 3. Adult Lace-necked Dove. Waikii, Hawaii. Elevation 4,700 feet above sea level; April 5, 1946.

abundant food, available either seasonally or locally, is primarily responsible for the best densities, but the possible factors believed to limit high dove populations are different for the two zones. Zone C_2 lies between 2,500 and 4,000 feet elevation, where the annual mean temperature is 60° F. and the average rainfall is between 40 and 60 inches annually. This temperature is lower than those in the best Lace-necked Dove zones and is suggested as possibly being able to inhibit high populations. Zone D_1, occurring between sea level and approximately 1,500 feet elevation, has an annual mean temperature of about 73° F. and an annual rainfall with a minimum of 60 inches. It is probable that the numerous and often heavy rains affect nesting success in this zone.

The poorest dove ranges occur in zones D_2, D_3, E_1, and E_2, which show low percentages of occupancy (5–21 per cent), poor populations (280–1,800), and generally low densities (50 or fewer birds per square mile). Zone D_2 lies between the general elevations of 1,500 and 4,000 feet, where the annual mean temperature is 60° F. and rainfall reaches 450 or more inches annually. Low temperatures, heavy rainfall, and the lush forest cover all prohibit high densities. Doves are found only where suitable foods occur in small openings cleared for cultivation or resulting from heavy grazing. The other three zones, D_3, E_1, and E_2, are above 4,000 feet elevation, where mean temperatures vary between 50° and 40° F. annually, and the extremes of rainfall are from about 100 inches at lower elevations to less than 40 inches at higher elevations. The cold temperatures probably contribute largely to the prevailing poor densities, but at lower elevations (D_3) the heavy rainfall is another adverse factor. Dove foods are extremely limited in these zones and water is unavailable in E_1 and E_2.

Nearly all informed persons interviewed during this survey expressed the opinion that Lace-necked Doves have been decreasing in recent years. Many believe that competition for food between this species and the more plentiful and more recently introduced Barred Dove, *Geopelia striata striata* (L.), is the cause of this decrease but data from our food studies given below indicate otherwise. It may be significant that on Hawaii, where the Barred Dove is just becoming established in only a few localized areas, the same island-wide decrease of the Lace-necked Dove is also reported.

FOODS

An analysis was made of Lace-necked Dove foods from 146 crops and 71 gizzards. Each food species in the crop was identified, separated, measured in cubic centimeters, totaled by aggregate volume, and recorded for occurrence. Gizzard contents were identified and recorded for occurrence only. Every month except January and all islands except Niihau and Kahoolawe were represented in the sample. Except for four doves, all were collected between sea level and 2,700 feet elevation in zones A, B, C_1, C_2, and D_1, and

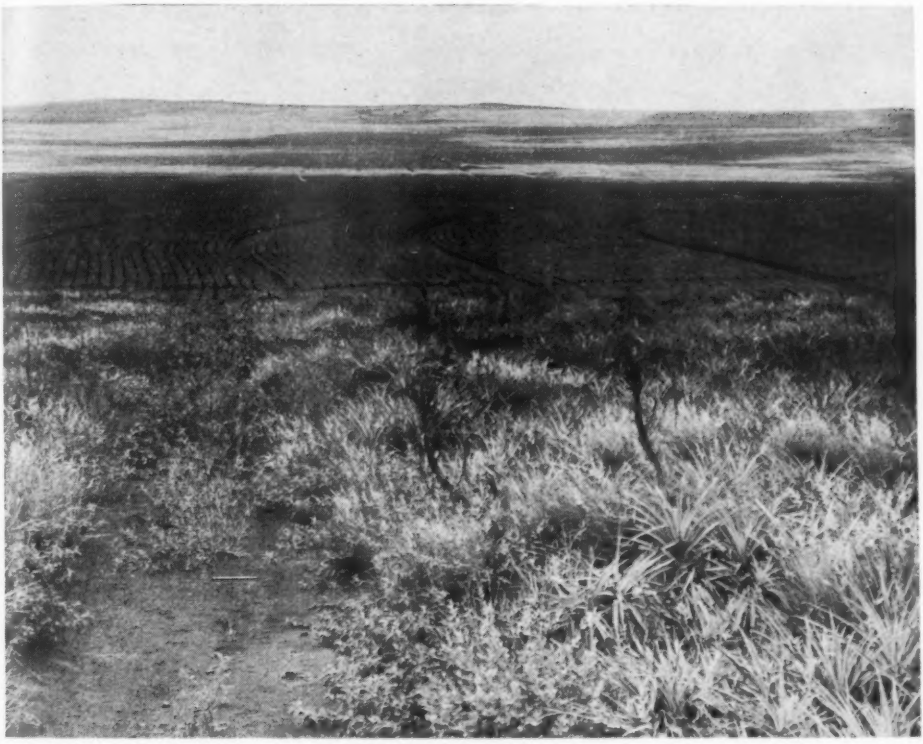


FIG. 4. Lace-necked Doves frequently feed in the fallow sections (foreground) of pineapple fields which support a rich growth of herbaceous annuals. The cultivated pineapple fields (background) are seldom utilized by this species. Lanai. Vegetation zone B, elevation 1,500 feet above sea level; August 27, 1946.

from the distribution of the food species in the Islands, it was obvious that feeding occurred almost entirely within this area. No great seasonal difference occurs in the food supply of doves in Hawaii although there may be periods when individual plant species produce seeds more abundantly, especially following rains in the drier regions. This food analysis was not made according to vegetation zone, as was done for most other game birds during this survey, for two reasons: Some doves collected on flyways were suspected of having fed in a vegetation zone different from the one in which they were taken; also, only a few zones which comprise dove range in the lower elevations are used in this food analysis.

Table 2 lists the foods of the Lace-necked Dove in Hawaii. Sixty-five plant species form 99.5 per cent of the diet and 13 animal items constitute the remaining 0.5 per cent. Of the plant foods, seeds and pods form 84.1 per cent, succulent fruits constitute 14.4 per cent, and roots and seedlings comprise the remaining 1.0 per cent. The nine most important foods on the basis of volume and and frequency of occurrence in crops (more than 2 per cent or more than 14 occurrences) are discussed briefly.

Momordica Balsamina L., balsam apple, is an exotic member of the family Cucurbitaceae and forms 23 per cent of the foods taken. It occurred in 43 (29 per cent) of the crops and 16 (22 per cent) of the gizzards. Although its

TABLE 2

FOODS OF THE LACE-NECKED DOVE IN HAWAII

SPECIES AND PARTS EATEN	PERCENTAGE CROP VOLUME	NUMBER OCCURRENCES IN 146 CROPS	NUMBER OCCURRENCES IN 71 GIZZARDS	ABUNDANCE OF FOOD BY VEGETATION ZONE*								
				A	B	C_1	C_2	D_1	D_2	D_3	E_1	E_2
PLANTS	99.5											
Momordica Balsamina, balsam apple; seed	23.1	43	16		o	o						
Waltheria americana, uhaloa; seed	17.6	57	27	o	c	c	o					
Cajanus Cajan, pigeon pea; seed	12.8	21	4		r	o	r	r				
Solanum nodiflorum, popolo; fruit, seed	10.0	19	11		o	c		o				
Lantana Camara, lantana; fruit, seed	9.6	7	7	o	a	c		o				
Wikstroemia phillyraefolia, akia; fruit, seed	4.4	5	3		r	o						
Portulaca sclerocarpa, ihimakole; seed, pod	3.7	17	0		r							
Dianella sandwicensis, ukiuki; fruit, seed	3.1	1	1					o	o			
Sida sp. (*cordifolia*), ilima; seed and *Sida* sp. (*fallax*), ilima; seed†	2.9	32	10	o c	c a	r c						
Hordeum vulgare, barley; seed	1.9	1	1				r					
Centaurea melitensis, Maltese thistle; seed	1.3	7	3	o	o							
Unidentified seeds	1.1	16	6									
Euphorbia hypericifolia, graceful spurge; seed	0.9	5	4		o	o						
Grevillea robusta, silk oak; seed	0.9	3	3		o	c						
Ananas comosus, pineapple; root	0.9	3	1	cultivated								
Zea mays, corn; seed	0.8	4	1	cultivated								
Aleurites moluccana, kukui; seed	0.7	1	1			o		c	c			
Verbena litoralis, verbena; seed	0.7	2	2		o	c	c				c	
Phytolacca octandra, pokeberry; fruit	0.4	4	5		r	r						
Atriplex semibaccata, Australian salt bush; seed	0.4	4	2	c	r							
Euphorbia geniculata, wild euphorbia; seed	0.3	1	1			o	o					
Opuntia megacantha, panini or cactus; seed	0.3	2	4	o	c	o						
Prosopis chilensis, algaroba or kiawe; seed pod, seedling	0.3	3	2	a	c							
Sida rhombifolia, ilima; seed	0.3	8	5		o	r						
Euphorbia hirta, garden spurge; seed	0.2	4	1		o	c						
Avena fatua, wild oat; seed	0.1	1	0		r	r	c					
Carica papaya, papaya; seed	0.1	1	0	cultivated								
Eugenia Cumini, Java plum; fruit	0.1	2	1		o	o		o				
Portulaca cyanosperma, small pigweed; seed	0.1	1	1	c								
Ricinus communis, castor bean; seed	0.1	1	1		o	o	r					
Siegesbeckia orientalis, small yellow crown beard; seed	0.1	6	5			o		r				
Tephrosia purpurea, ahuhu; seed	0.1	13	5	o	r							

*From Ripperton and Hosaka (1942). a = abundant; c = common; o = occasional; r = rare.

†The seeds of these species are practically indistinguishable, hence they are combined herein.

TABLE 2 (Continued)
FOODS OF THE LACE-NECKED DOVE IN HAWAII

SPECIES AND PARTS EATEN	PERCENTAGE CROP VOLUME	NUMBER OCCURRENCES IN 146 CROPS	NUMBER OCCURRENCES IN 71 GIZZARDS	ABUNDANCE OF FOOD BY VEGETATION ZONE*								
				A	B	C_1	C_2	D_1	D_2	D_3	E_1	E_2
PLANTS continued												
Xanthium saccharatum, cocklebur; seed	0.1	1	0	o	c	o						
Unidentified seedling	0.1	1	0									
Abutilon molle, mao; seed	T	5	3	r	o							
Amaranthus hybridus, spleen amaranth; seed	T	6	2		o	o						
Argemone alba var. *glauca*, puakala; seed	T	4	0	o	c							
Bidens pilosa, pilipili; seed	T	1	1	o	c	c	o	o	r			
Brassica sp., mustard; seed	T	2	0									
Cassia occidentalis; seed	T	1	0		o	o		r				
Casuarina sp., ironwood; seed	T	2	1									
Chenopodium ambrosioides, Mexican tea; seed	T	1	1		r						r	
Cirsium vulgare, common thistle; seed	T	3	3			o	c				o	
Cuphea carthagenensis, tarweed; seed pod	T	1	0			o		c	o			
Dodonaea viscosa, aalii; seed	T	6	14		o	o	o				o	
Echinochloa crusgalli var. *crus-pavonis*, barnyard grass; seed	T	1	0		c	c						
Eleusine indica, wire grass; seed	T	1	0		r	o		r				
Fungus, puff ball	T	1	0									
Geranium carolinianum var. *australe*, wild geranium; seed	T	1	1				c		o	o	r	
Ipomoea sp.; seed	T	1	0									
Leucaena glauca, koa haole; seed	T	1	0	c	a	c		o				
Malva parviflora, little mallow; seed	T	1	2		o	c	o					
Malvastrum coromandelianum, false mallow; pod, seed	T	1	1	o	c							
Mimosa pudica, sensitive plant; seed	T	1	1			o		c	r			
Portulaca oleracea, pigweed; seed, pod	T	1	0	r	o	c		o				
Setaria verticillata, bristly foxtail; seed	T	3	3	c	o	o						
Sporobolus capensis, rattail; seed	T	1	2		r	o	c			o	o	
Triticum aestivum, wheat; seed	T	1	0		imported		cattle		feed			
Cassia Leschenaultiana, Japanese tea; seed	0	0	4		c	c		r				
Chenopodium oahuense, aweoweo; seed	0	0	1		o	o					o	
Desmodium uncinatum, Spanish clover; seed	0	0	2		r	c	c	c	r		r	
Indigofera suffruticosa, indigo; seed	0	0	1		r	c	o	r				
Paspalum Urvillei, vasey grass; seed	0	0	1			r	r	r				
Plantago sp.; seed	0	0	1									
Psidium Guajava, guava; seed	0	0	5		o	c		a	o			
Styphelia Tameiameiae, puakeawe; seed	0	0	3			o	o				o	o

TABLE 2 (Continued)
FOODS OF THE LACE-NECKED DOVE IN HAWAII

SPECIES AND PARTS EATEN	PERCENTAGE CROP VOLUME	NUMBER OCCURRENCES IN 146 CROPS	NUMBER OCCURRENCES IN 71 GIZZARDS	ABUNDANCE OF FOOD BY VEGETATION ZONE[a]								
				A	B	C_1	C_2	D_1	D_2	D_3	E_1	E_2
ANIMALS	0.5											
Megacerus alternatus, pea weevil; adult	0.2	10	0									
Carpophilus humeralis, yellow-shouldered souring beetle; adult	0.2	3	2									
Carpophilus hemipterus, dried fruit beetle; adult	0.1	3	2									
Antonina graminis, scale insect; fragment	T	2	0									
Blattidae (unidentified), cockroach; egg case	T	7	0									
Cirphis unipuncta, army worm; larva	T	1	0									
Coccidae (unidentified), scale insects; adult	T	1	0									
Coleoptera (unidentified), beetles; adult	T	1	0									
Conoderus exsul, wireworm; larva, pupa	T	4	0									
Crustacea (unidentified), crayfish; chitin	T	1	0									
Lepidoptera (unidentified), butterflies, moths, skippers; larva	T	1	0									
Mollusca (unidentified), aquatic snail; shell	T	1	0									
Rodentia (unidentified), rodent; tooth	T	1	0									

general distribution is only occasional in zones B and C_1, it grows very profusely during all seasons in certain areas, particularly in fallow pineapple fields and along roadsides. Lace-necked Doves show a preference for the large seeds, and concentrations of feeding birds occur where this plant is abundant and in seed.

Waltheria americana L., or uhaloa, comprising 17 per cent of the entire diet, ranks as an important food. Its seeds occurred in 57 (39 per cent) of the crops and 27 (38 per cent) of the gizzards. Uhaloa grows occasionally in zones A and C_2 but commonly in B and C_1. This exotic member of the Sterculiaceae appears to produce seeds abundantly throughout the year. Widely available in arid sections at low elevations, this plant apparently plays a prominent role as a food in these regions where seed productivity is otherwise low. We also found uhaloa to be an important food of the Barred Dove and the California Quail (*Lophortyx californica*) in Hawaii.

Cajanus Cajan (L.) Millsp., pigeon pea, constitutes 12 per cent of the Lace-necked Doves' food. Twenty-one (14 per cent) of the crops and 4 (5 per cent) of the gizzards contained these seeds. This exotic legume is rare in zones B, C_2, and D_1, but occasional in zone C_1, where it occurs chiefly as cultivated cattle forage. Seeds are available throughout the year.

Solanum nodiflorum Jacq., or popolo, grows occasionally in zones B and D_1 but commonly in zone C_1, particularly in old pineapple fields. The fruit and seeds of this indigenous species of the Solanaceae comprised 10 per cent of the diet and occurred in 19 (13 per cent) of the crops and 11 (15 per cent) of the gizzards. Field observations show that doves often gorge themselves on these succulent fruits, which are available all year. It is possible that moisture provided by this fruit may entirely eliminate the need for surface drinking water. Popolo is also an important food of pheasants (*Phasianus torquatus* Gmelin and *P. versicolor* Veillot) in Hawaii.

Lantana Camara L. is an exotic verbena which accounted for 9 per cent of the diet. The fruits and seeds were taken in only 7 (4 per cent) of the crops and 7 (9 per cent) of the gizzards. *Lantana* is abundant in zone B, common in C_1, and occasional in A and D_1, and this distribution makes it widely available throughout dove range. However, its relatively infrequent occurrence and small volume in the diet implies that it is not a generally preferred food. Almost the entire volume of this plant in the food analysis came from four Lace-necked Doves taken at Koloa, Kauai, in zone C_1. Two Barred Doves collected at the same place and time had also eaten large quantities of *Lantana* although it was not a common food of Barred Doves. Possibly the *Lantana* here was particularly attractive at this time or other foods may have been lack-

FIG. 5. The dense coastal stands of algaroba (*Prosopis chilensis*) furnish good roosting and nesting sites for the Lace-necked Dove. Openings as shown in the foreground support food species such as uhaloa (*Waltheria americana*), ilima (*Sida* sp.), and *Lantana Camara*. Kekaha, Kauai. Vegetation zone A, sea level; October 6, 1946.

ing. Perkins and Swezey (1934) have accredited the Lace-necked Dove with being a principal agent in the wide dissemination of *Lantana* throughout coastal areas. However, the limited feeding on *Lantana* and the fact that all *Lantana* seeds in gizzards were ground up indicates to us that Lace-necked Doves may have contributed little to the spread of this noxious shrub. Probably of greater importance in permitting its spread in the Islands was the lack of natural checks on this exotic plant in its new environment.

The seeds and fruits of *Wikstroemia phillyraefolia* Gray, locally known as akia, were utilized by Lace-necked Doves as 4 per cent of the diet. They occurred in 5 (3 per cent) of the crops and 3 (4 per cent) of the gizzards. The small volume and rare occurrence in the diet are probably related to the distribution of akia, which is rare in zone B and occasional in C_1. However, on certain lava outcrops in zone C_2 on Hawaii, this endemic species of the Thymelaeaceae is abundant and is believed to be a preferred food because of its intensive utilization by Lace-necked Doves there. The fruits of this plant, too, furnish a ready supply of moisture. Akia, obtainable during all seasons but most abundantly during spring, summer, and fall, also ranks as an important food of pheasants and feral pigeons (*Columba livia* Gmelin) in Hawaii.

Portulaca sclerocarpa Gray, or ihimakole, formed 3 per cent of the food of Lace-necked Doves. It occurred in 17 (11 per cent) of the crops but in no gizzards. Both seed pods and seeds of this endemic species of the Portulacaceae are fed upon in zone B, where it occurs rarely.

Dianella sandwicensis Hook. and Arn., or ukiuki, grows occasionally in zones D_1 and D_2. The crop and gizzard of only one bird contained seeds and fruits of this plant, which amounted to 3 per cent of the total foods. This bird was taken from zone D_3 at Kokee, Kauai, where the ukiuki fruits abundantly during summer and fall. Doves in this section have been observed to feed upon the seeds and fruits of this species but because of its limited distribution and the scarcity of Lace-necked Doves in this zone, it cannot be considered a major food. This endemic lily is an important food of pheasants and Jungle Fowls (*Gallus gallus* (L.)) in this area.

Sida cordifolia L. and *Sida fallax* Walpers, both called ilima, are indigenous species of the family Malvaceae. Because their seeds are practically indistinguishable, their utilization has been combined as 2 per cent of the Lace-necked Doves' food. These plants occurred in 32 (21 per cent) of the crops and 10 (14 per cent) of the gizzards. The former species is occasional in zone A, common in B, and rare in C_1, while the latter is common in zones A and C_1 and abundant in B. These species produce seeds abundantly throughout the year although during some drouth periods production is slackened. They, combined with uhaloa, provide a desirable combination of foods in drier and more barren parts of dove range.

The remaining plant and animal foods appear to be of less importance because of their small volumes and the infrequencies of their occurrence in the diet. However, as contributions to variety and to nutrition they are doubtless of value. Most plants in this group are widely available in areas from which birds were collected. In many parts of the range there is apparently sufficient food to support higher dove populations than now exist.

Grit occurred in 17 crops and 38 gizzards and averaged 0.3 cubic centimeter in both cases; 10 additional gizzards had traces of grit while 23 had none. Both angular and well-rounded pieces of feldspar, olivine, basalt, quartz, bottle glass, opaline, and round concretions of hard earth, from 1 to 4 millimeters in diameter, were found.

FEEDING, WATERING, AND ROOSTING HABITS

Feeding is occasional from an hour or more after daylight until about noon, when it is

greatly accelerated. In those areas of abundant food far removed from roosting sites, Lace-necked Doves infiltrate irregularly throughout the morning, reaching an apparent maximum number about noon. Heaviest feeding takes place during the next few hours. Beginning about 3:00 P.M. birds with full crops (averaging 10.1 cubic centimeters in 85 birds with a maximum of 35.1 cubic centimeters) start returning singly or in groups of twos or threes along definite flyways to their roosting sites. Distances of at least 5 miles are often traveled between feeding grounds and communal, coastal roosting sites but doves may reside in certain roosting areas with available food.

Lace-necked Doves and Barred Doves often feed in the same fields, giving rise to the local opinion that serious competition for foods occurs between these species. However, Lace-necked Doves select principally large seeds and fruits while Barred Doves utilize small-seeded, rapidly maturing annuals and grasses (Schwartz and Schwartz, 1949). As a result of these food preferences, the use of these fields by each species is generally at different stages of cultivation or plant succession. Although some of the foods eaten by both doves may be of the same species, it is highly significant that only one plant, uhaloa, is an important food in the diet of both birds. This shrub occurs in great abundance throughout most dove range and the seeds are more than ample to supply the needs of both species of doves as well as of other game birds which also utilize them.

Our observations indicate that either fresh or brackish surface water or succulent fruit is a prerequisite for good Lace-necked Dove range. Birds resident in areas without available surface water appear to substitute succulent fruits in fulfilling their daily water needs. Elsewhere, doves readily utilize cattle troughs (especially overflow or seeps), irrigation ditches, reservoirs, pools, streams, and springs, in addition to rainfall and dew which may collect in the leaf axils of many plants. The proximity of these water sources to feeding and roosting areas plays an important role in the daily range. Customarily, Lace-necked Doves use water close to their feeding area in late afternoon but in the morning resort to a water source near their roosts. At these latter sites they may linger and bathe and preen their feathers before venturing out to their foraging grounds for the day. In some dry sections, existing water holes now attract doves over approximately a 5-mile radius. The presence of water within flying range of the nest has been shown by Arnold (1943) to be a necessity for the western White-winged Dove, *Zenaida asiatica mearnsi* (Ridgway), and it is not unlikely that a similar requirement holds for the Lace-necked Dove in Hawaii.

Roosting areas are usually dense wooded thickets of algaroba on the coastal flats, dense groves of *Eucalyptus* sp. or of ironwood (*Casuarina* sp.), or the peripheries of forested areas and wooded draws radiating therefrom, although some roosting occurs in practically any timbered area. In some parts of the Islands, Lace-necked Doves tend to be gregarious in their roosting habits, and the commonest community roosting sites in the dense coastal stands of algaroba harbor nightly populations of a hundred or more birds per acre.

BREEDING

From the little evidence accumulated during this survey, we believe that Lace-necked Doves breed mostly from February through September and possibly, to a limited extent, during the entire year.

We noticed that the "cooing" song of the males becomes greatly accelerated during January and for the next 2 months is increasingly obvious during the early morning hours and to a lesser extent during the day. After a peak from mid-March through mid-July, the intensity of "cooing" in the general population gradually diminishes until by late October occasional courting songs are heard

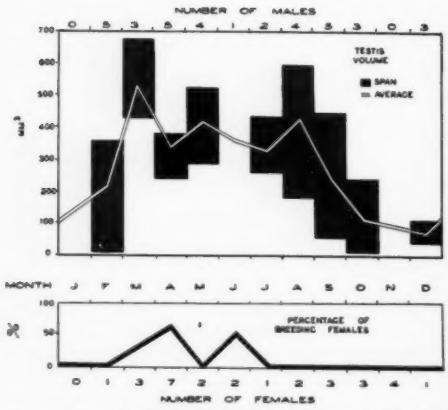

NUMBER OF MALES
0 5 3 5 4 1 2 4 5 3 0 3
TESTIS VOLUME
SPAN
AVERAGE
MONTH J F M A M J J A S O N D
PERCENTAGE OF BREEDING FEMALES
0 1 3 7 2 2 1 2 3 3 4 1
NUMBER OF FEMALES

FIG. 6. Breeding of the Lace-necked Dove in Hawaii.

only in early morning. These variations in vocal activity generally coincide with fluctuations in testis volumes (roughly computed by multiplying length × width × depth of both testes per individual) of 35 collected adult males, and with indications of breeding (determined by the presence of maturing Graafian follicles) in 29 collected adult females (Figure 6). We do not believe that breeding is common after September, as evidenced by the fact that 86 birds collected from October through December all were in adult plumage.

In southern China, the breeding season of the species *S. chinensis* is spring, summer, and autumn (La Touche, 1931–34) and in India these doves are reported to breed throughout the year (Ali, 1944) and probably to raise several broods annually (Whistler, 1935). Breeding of this species in the Malay Peninsula generally extends from January to March, but extremes from November to May occur (Robinson and Chasen, 1936).

In Hawaii, the Lace-necked Dove shows a wide selection of nesting sites. Typical ones observed during this survey are as follows: (1) in a strong crotch 10 feet above the ground in an algaroba tree; (2) 35 feet above the ground in the outer branches of an algaroba tree; (3) in a clump of cactus (*Opuntia megacantha*) on a sloping stem 6 feet above

FIG. 7. A Lace-necked Dove nest in puakeawe (*Styphelia Tameiameiae*). Kapapala, Hawaii. Vegetation zone C_2, elevation 4,000 feet; June 8, 1946.

the ground; (4) in a thicket of *Smilax* sp. and akala (*Rubus hawaiensis*) growing on the rim of a gulch 25 feet deep; (5) 18 feet above the ground in the outer fringes of a mamani tree (*Sophora chrysophylla*); (6) 5 feet above the ground in a puakeawe bush (*Styphelia Tameiameiae*); (7) 35 feet above the ground in the outer branches of an ironwood tree.

The nest is typically dove-like, consisting

FIG. 8. Juvenile Lace-necked Dove. Note the lack of the neck "lace" so characteristic of the adult. Honolulu, Oahu. Sea level; May 15, 1946.

of a flimsy platform about 7 inches in diameter, roughly constructed of twigs between ⅛ and ¼ inch in diameter and about 4 or 5 inches long. Sometimes it contains a lining of fine rootlets for the two white eggs.

The juvenile plumage lacks the black and white neck "lace" so characteristic of the adult, and the contour feathers are distinctly and narrowly light-tipped. Three nest-free birds in juvenile plumage had bursae of Fabricius 4 to 5 millimeters in length. Thirteen birds in adult plumage had no measurable bursae while two others had bursae measuring 3 and 5 millimeters, respectively. Riddle (1928), working with other species of *Streptopelia*, found that bursae usually, but not invariably, involuted at sexual maturity.

SEX RATIOS, WEIGHTS, AND MEASUREMENTS

Sex ratios found in the Lace-necked Dove in Hawaii are as follows:

	NUMBER OF MALES	NUMBER OF FEMALES	MALES PER 100 FEMALES
79 adult and nest-free juvenile doves	43	36	119:100
64 adults	35	29	120:100
15 juveniles	8	7	114:100

Three adult males averaged 146 grams and three adult females averaged 159 grams in weight. This small series indicates that females may be heavier than males. However, measurements of 59 adult Lace-necked Doves show males to be slightly larger than females (Table 3).

PARASITES

Lice were the only external parasites observed on Lace-necked Doves and infestations were light to moderate. *Goniodes* sp. larvae, *Goniodes chinensis* Kell. & Chap., and a new species of *Columbicola*, not yet described, occurred on collected birds. The latter two species were also identified from Barred Doves in Hawaii.

Intestinal roundworms, *Ascaridia columbae* (Gmelin), were found occasionally, thus establishing a new host record for this parasite. *A. columbae* also occurred in feral pigeons in Hawaii. We found the eyeworm, *Oxyspirura mansoni* Cobbold, in Lace-necked Doves, as did Alicata (1947), and in the Japanese Quail (*Coturnix coturnix japonica* Temminck and Schlegel), and in pheasants in Hawaii. The heaviest infestation was two worms in each eye of a single dove. *Subulura brumpti* (Lopez Neyra), a cecal roundworm, occurred in a single specimen. This parasite is common in Japanese Quail and pheasants in Hawaii. Known intermediate hosts of the latter two parasites were not found in this food habits study, but doubtless are consumed by the Lace-necked Dove.

The cestode *Davainea crassula* (Rudolphi) was found in the Lace-necked Dove; this is another new host record. It also occurred in feral pigeons in Hawaii. Infestations varied from light to extremely heavy. The intermediate host of this parasite is unknown but since the diet of Lace-necked Doves includes some insects and mollusks, it is possible that

TABLE 3

AVERAGE MEASUREMENTS IN MILLIMETERS OF 59 ADULT LACE-NECKED DOVES

MEASUREMENTS	33 ADULT MALES	26 ADULT FEMALES
Total length	324.0	318.4
Extent of wing	459.4	451.0
Length of closed wing	152.4	150.0
Length of tail	145.6	141.5
Exposed culmen	17.4	16.8
Length of middle toe including nail	25.4	25.3

infestations with this cestode may occur as a result of consumption of these food forms.

ACKNOWLEDGMENTS

These observations were made during a survey of the game birds in the Hawaiian Islands as the initial step in the Federal Aid-Wildlife Program (1-R) of the Board of Commissioners of Agriculture and Forestry, Territory of Hawaii. Field work was carried out from February, 1946, through July, 1947.

We are indebted in many ways to fellow workers with the Board of Commissioners of Agriculture and Forestry, particularly Mr. C. G. Lennox, President of the Board, and Mr. V. E. Brock, Director, Division of Fish and Game; and to the owners and operators of many of the ranches and sugar cane and pineapple plantations in Hawaii.

For especial assistance we wish to thank: Dr. E. Mayr, American Museum of Natural History, for examining collected Lace-necked Doves; Mr. E. Y. Hosaka, University of Hawaii and Bernice P. Bishop Museum, Mr. G. O. Fagerlund, formerly of Hawaii National Park and now with Olympic National Park, and Dr. H. St. John, University of Hawaii, for identification of certain plants and for plant taxonomy; Mr. C. E. Pemberton, Hawaiian Sugar Planters' Association Experiment Station, for identification of insects; Dr. E. W. Stafford of the United States Department of Agriculture, Mr. E. Ediger, United States Fish and Wildlife Service, and Dr. J. E. Alicata, University of Hawaii, for identification of parasites; Dr. R. W. Hiatt, University of Hawaii, Mr. L. W. Wishard, Honokaa Sugar Company, and Judge M. Pence of Hilo, Hawaii, for supplying some of the crops used in the food analysis; and Mr. W. O. Nagel, Missouri Conservation Commission, for critically reading this manuscript.

SUMMARY

1. Lace-necked Doves (*Streptopelia chinensis chinensis*) are permanent residents on all of the major Hawaiian Islands. A total of 3,120 square miles is occupied by an estimated 88,680 Lace-necked Doves with densities varying from less than 10 to 200 birds per square mile. The range occurs mostly from sea level to 4,000 feet elevation but in one area on Hawaii it reaches 8,000 feet. All types of land except dense forests and barren lava support doves. The optimum range occurs from sea level to 2,500 feet elevation. Here, the mean annual temperature is between 75° and 70° F. and extremes in the annual rainfall are from less than 10 to approximately 60 inches. Where rainfall is greater and/or temperatures lower, lesser populations occur.
2. An analysis of foods in 146 crops shows that 65 plant species comprise 99.5 per cent of the diet while 13 animal items constitute the remaining 0.5 per cent. Of the plant matter, seeds and pods amount to 84.1 per cent, succulent fruits 14.4 per cent, and roots and seedlings 1.0 per cent. Grit occurred in 17 crops and 38 gizzards, averaging 0.3 cubic centimeter in each case. Feeding activity is greatest from approximately noon to 3:00 P.M. No competition for food occurs between Lace-necked and Barred Doves in Hawaii.
3. Either fresh or brackish surface water or succulent fruit is a prerequisite for good Lace-necked Dove range.
4. Lace-necked Doves may fly as far as 5 miles between roosting and feeding areas but favorable sites with both available food and good roosting cover have resident populations.
5. Roosting areas are usually densely wooded thickets along the coastal flats, occasional dense groves, or the peripheries of forested areas and wooded draws radiating therefrom, but some roosting occurs in practically any timbered area.
6. Lace-necked Doves breed mostly from February through September and pos-

sibly to a limited extent during the entire year.

7. The juvenile plumage lacks the black and white neck "lace" so characteristic of the adult and contour feathers are distinctly light tipped.
8. The sex ratio in 79 adult and nest-free juvenile doves was 43 males to 36 females or 119:100. Weights of 6 adults and measurements of 59 adults are given.
9. Lice externally and roundworms in the intestine, eye, and caecum occurred generally in light infestations. Tapeworm parasitism varied from light to extremely heavy.

REFERENCES

ALI, S. 1944. *Book of Indian birds*. Ed. 3. 438 pp. Bombay Natural History Society.

ALICATA, J. E. 1947. Parasites and parasitic diseases of domestic animals in the Hawaiian Islands. *Pacific Sci.* 1 (2): 69–84.

ARNOLD, L. W. 1943. *The western white-winged dove in Arizona*. Ariz. Fish and Game Comn. 92 pp.

CAUM, E. L. 1933. *The exotic birds of Hawaii*. Bernice P. Bishop Mus., Occas. Papers 10 (9): 1–55.

FISHER, H. I. MS. The avifauna of Niihau Island, Hawaiian Archipelago. *Condor*. (In Press.)

LA TOUCHE, J. D. D. 1931–34. *Handbook of the birds of Eastern China*. Vol. 2, 566 pp. Taylor and Francis, London.

PERKINS, R. C. L., and O. H. SWEZEY. 1934. The introduction into Hawaii of insects that attack *Lantana*. *Hawaii. Sugar Planers' Assoc. Expt. Sta., Bul. Ent. Ser.* 16: 83 pp.

RIDDLE, O. 1928. Studies on the physiology of reproduction in birds. XXIII. Growth of the gonads and Bursa Fabricii in doves and pigeons with data for body growth and age at maturity. *Amer. Jour. Physiol.* 86: 248–265.

RIPPERTON, J. C., and E. Y. HOSAKA. 1942. *Vegetation zones of Hawaii*. Hawaii Agr. Expt. Sta. Bul. 89, 61 pp.

ROBINSON, H. C., and F. N. CHASEN. 1936. *Birds of the Malay Peninsula*. Vol. 3, 264 pp. H. F. and G. Witherby, Ltd., London.

SCHWARTZ, C. W., and E. R. SCHWARTZ. 1949. *The game birds in Hawaii*. 168 pp. Hawaii Bd. Commrs. Agr. and Forestry, Honolulu.

———and——— 1950. The California quail in Hawaii. *Auk* 67: 1–38.

WHISTLER, H. 1935. *Popular handbook of Indian birds*. 513 pp. Guerney and Jackson, London.

NOTES

Two Juvenile Pointed-tailed Ocean Sunfish, *Masturus lanceolatus*, from Hawaiian Waters

OSEPH E. KING[1]

The pointed-tailed ocean sunfish, *Masturus lanceolatus* (Liénard), is one of the "rare" marine fishes although it has been recorded from the tropical and subtropical areas of all oceans. In Gudger's review (1937*b*) of the natural history and distribution of the species, he reported only 59 authenticated records of the fish in the hundred years after its discovery in 1836. Strangely enough, of these 59 individuals there were 28 young and 31 adults, with no examples between the largest small specimen (60 mm. or 2.4 inches, standard length) and the smallest large specimen (30.5 inches, total length). Brimley (1939) has supplied records of five adult fish, ranging in size from 28 to 83 inches, that were not included in Gudger's report; four of these fish were from North Carolina waters, the fifth from Florida.

This wide gap between larval fish and adults was partially filled when three 6-inch juvenile fish were obtained from the stomach of a dolphin, *Coryphaena hippurus* L., taken in Florida waters (Gudger, 1938). Kuronuma (1940) described a juvenile *M. lanceolatus*, taken in a gill net in Japanese waters, which was 145 mm. in length from snout to caudal base and 259 mm. from snout to end of caudal fin. This interesting specimen differed from any previously described in that the caudal lobes was extended as a thin filament equal to approximately half the total body length.

Recently, Fitch (1950) reported that *M. lanceolatus* is found quite commonly in the stomachs of yellowfin tuna taken in Hawaiian waters, nearly a hundred specimens varying in size from ¼ inch to 2 inches having been obtained from this source. The only previous record of the species for Hawaiian waters is that of an adult fish, 37.3 inches in length, obtained from the Honolulu fish market in 1919 (Fowler, 1928).

The author has been unable to find in the literature any reports, except that of Kuronuma (1940), which describe or figure the caudal fin of *M. lanceolatus* as having more than a short lobe-like extension which may be pointed in the very young but in the adults is usually frayed or mutilated. From this characteristic shape of the caudal fin the fish has derived its scientific name, *Masturus lanceolatus* [Gr., *mastos*, breast or nipple; Gr., *oura*, tail; L., *lanceolatus*, a little lance = the nipple-tailed, lance-tailed fish (Gudger, 1937*a*)].

On April 11, 1950, during long-line fishing for tuna by the Fish and Wildlife Service research vessel *Hugh M. Smith*, a dolphin (1,100 mm. fork length) was taken just west of the island of Hawaii at 19° 30′ N. Lat.–156° 05′ W. Long. In the dolphin's stomach were two 5-inch *M. lanceolatus*, one in good condition, the other with a gash on each side. Both specimens (in alcohol) are generally similar in coloration to the 6-inch fish described by Gudger (1938). They are dark gray dorsally, shading into milky-white on the lower two-thirds of the body. They have the typical gray spotting below the eyes and pectoral fins and posteriorly above the anal fin.

[1]Fishery Research Biologist, Pacific Oceanic Fishery Investigations, U. S. Fish and Wildlife Service, Honolulu, T. H. Manuscript received July 7, 1950.

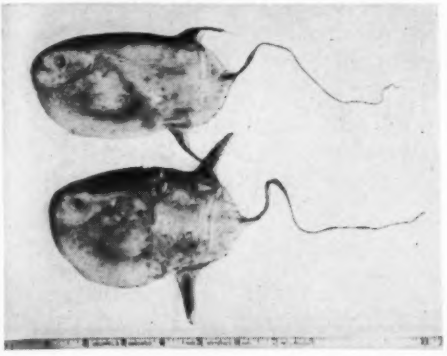


FIG. 1. Two juvenile *Masturus lanceolatus* taken from the stomach of a dolphin captured in Hawaiian waters. April 11, 1950.

These fish differ in one important respect, however, from any previously collected. Each has the caudal lobe continued as a whip-like structure longer than the body of the fish (Fig. 1). Except for the proximal 2 or 3 centimeters, this caudal extension is very fragile, almost paper-thin, and is frayed toward the tip. These may be the first observed specimens—at least among the post-larvae, juveniles, and adults—to show the true "normal" or unmutilated nature of the caudal fin. In view of the delicate structure of this appendage it is easily seen why the appendage is usually greatly reduced or missing in juvenile and adult specimens.

Measurements of the two fish, fin ray counts, etc., are given in the accompanying table:

REFERENCES

BRIMLEY, H. H. 1939. The ocean sun-fishes on the North Carolina coast. The pointed-tailed *Masturus lanceolatus* and the round-tailed *Mola mola*. *Jour. Elisha Mitchell Sci. Soc.* 55(2): 295–303.

FITCH, JOHN E. 1950. Notes on some Pacific fishes. *Calif. Fish and Game* 36(2): 65–73.

FOWLER, HENRY W. 1928. *The fishes of Oceania*. Bernice P. Bishop Mus., Mem. 10: 1–540.

GUDGER, E. W. 1937*a*. The structure and development of the pointed tail of the ocean sunfish, *Masturus lanceolatus*. *Ann. and Mag. Nat. Hist.* XIX (10): 1–46.

——— 1937*b*. The natural history and geographical distribution of the pointed-tailed ocean sunfish (*Masturus lanceolatus*) with notes on the shape of the tail. *Zool. Soc. London, Proc.* Ser. A, Pt. 3, 353–396.

——— 1938. Three six-inch pointed-tailed ocean sunfish, *Masturus lanceolatus*, the largest post-larvae on record. *Jour. Elisha Mitchell Sci. Soc.* 55(2): 305–313.

KURONUMA, KATSUZO. 1940. A young ocean sunfish, *Mola mola*, taken from the stomach of *Germo germo*, and a specimen of *Masturus lanceolatus* as the second record from Japanese water. *Biogeogr. Soc. Japan, Bul.* 10(2): 25–28.

TABLE 1

MEASUREMENTS AND FIN-RAY COUNTS OF TWO JUVENILE POINTED-TAILED OCEAN SUNFISH (LENGTH AND DEPTH IN MILLIMETERS)

SPECIMEN	LENGTH TO			DEPTH			FIN-RAY COUNT				
	Base C	Edge C	Tip C	Behind eye	Before D & A	Over D & A	P	D	C	A	D+C+A
Good condition	111.9	135.0	300	59.8	63.6	121	10	20 (19?)	5+6+8	19 (18?)	58
Gashes in both sides	107.2	129.0	317	68.2	68.6	135	10	19 (18?)	5+6+7	18	55

News Notes

A new edition of Utinomi's *Bibliographia Micronesica* is to be published soon by the University of Hawaii Press. The extensive bibliography, which is the most complete list yet compiled of references to scientific publications concerned with Micronesia, was first brought out by Dr. Huzio Utinomi in Tokyo in 1944. It attempted to include all papers published until that time in the Micronesian aspects of the various fields of botany, zoology, geology, geophysics, anthropology and ethnology (including geography and fisheries). It is therefore a polyglot publication, citing not only papers published in the major European languages but also the contributions of Japanese scientists published in Japanese.

Almost all the copies of the original edition were destroyed during the bombing of Tokyo in the last months of World War II, and the few surviving copies have become, quite literally, museum pieces.

The chordate section of the bibliography was published in Volume I, Number 3, of *Pacific Science*, the plan then being to run a portion of the bibliography in succeeding issues of the journal. When this plan proved unfeasible, the University of Hawaii Press, at the request of *Pacific Science* editors, agreed to publish the complete work.

Members of the University of Hawaii faculty have cooperated in translating into English the Japanese citations, helping to make available for the first time to Occidental scientists references to papers which otherwise might remain unknown to them because of their lack of knowledge of Japanese ideographs.

The task of achieving correct translations was eased considerably by Japanese-speaking students and scholars at the University of Hawaii and by Dr. Utinomi, himself, in Japan. With their help the titles of the cited papers and publications have been translated into English, and the names of the journals, books, and other sources in which they appear have been translated into English and transliterated into the Romanji equivalents of the Japanese characters.

The citations in other languages remain in their original form. To complete the usefulness of the bibliography, the lists of the journals, magazines, and other publications in which the various citations appear are also provided, as they are in the original edition, in two sections, one composed of publications issued in Japan, primarily in the Japanese language, the other made up of publications in the languages of the Occident.

The University of Hawaii Press edition of Utinomi's bibliography will be published at $2.50 under the title *A Bibliography of Micronesia*. It will contain approximately 150 pages, and will present the citations in a double-column format designed for the convenience of the user. A prepublication price of $2.00 will apply on all orders received prior to May 1, 1951, the tentative publication date. Copies may be ordered from the University of Hawaii Press, University of Hawaii, Honolulu 14, Hawaii, U.S.A.

KUENEN, PH. H. *Marine Geology*. viii + 568 pp., 2 pls., 246 figs. John Wiley & Sons, Inc., New York, and Chapman & Hall, Limited, London, 1950. $7.50.

Marine Geology, by Ph. H. Kuenen, Professor of Geology, University of Groningen, The Netherlands, is a very welcome textbook summary in a field where progress has been laborious and slow. Despite the chief reliance of the geologic time scale on marine stratigraphy, treatment of marine processes in most textbooks has been almost necessarily meager. Elementary geology, in America at least, has been taught largely to students who have scarcely seen the sea. Oceanographic knowledge has been gathered mostly by workers in physics, chemistry, and biology and unhappily lodged in massive expedition volumes. Great numbers of geologists have only become aware of the ocean and its problems while engaged in often unrelated work during the Pacific War.

Professor Kuenen's treatise first combines the noun "geology" with the adjective "marine." Substantial parts of the data used are common

to *The Oceans* of Sverdrup, Fleming, and Johnson and to *Submarine Geology* by Shepard, but in the aim and mode of treatment there is no significant overlap. Numerous tables and diagrams present a wealth of quantitative material from widely scattered sources, and the reader is impressed by the inclusion of published data up to 1948. One of the chief merits of the book is the degree to which presentation of basic data is followed through by analysis of many of geology's much-discussed questions such as the one of permanency of ocean basins. The book is very effectively illustrated; despite the profuse and not always discriminate use of halftones in the textbooks of the past half century, Kuenen has produced an altogether pleasing text without them.—C.K.W.

The following publications of the Natural Resources Section, General Headquarters, Supreme Commander for the Allied Powers, Tokyo, Japan, have been received. Each report includes a list of all the reports previously published, their distribution, and rules for obtaining them.

Whiteware Raw Material Resources of Japan. [By Donald E. Lee and Hideshiro Hasegawa.] Report No. 135. 61 pp., 19 figs., 57 tables.

The Japanese Village in Transition. [By Arthur E. Raper, Tamie Tsuchiyama, Herbert Passin, and David L. Sills.] Report No. 136. 272 pp., 50 figs., 38 tables, numerous photographs.

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